

THE BASES OF ANGIOSPERM PHYLOGENY: VEGETATIVE MORPHOLOGY¹

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ABSTRACT

Coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships are present in dicotyledonous leaves. Features of greatest value in assessing these affinities include leaf organization; marginal features, including morphology of the tooth; major vein configuration; characters of the intercostal venation; and gland placement. Of these, recognition of tooth morphology appears to be an overlooked tool of major systematic importance. Variation in these features is most coherent when analyzed in terms of the Takhtajan and Cronquist systems of dicot classification. Essential to our procedure was a recognition of the "basic" leaf features of each taxon. These were regarded as the most generalized type from which all of the more specialized types in a taxon could have been derived and they were derived from an analysis of the comparative morphology of modern leaves with limited input from the fossil record. The resulting scheme indicates strong correlation of leaf features with six of the seven Takhtajan subclasses, in addition to paralleling and clarifying both systems at the ordinal and familial levels. Conspicuous exceptions are the breakdown of the Asteridae into a possible rosid and a possible dilleniid group, reassignment of the Celastrales and Myrtales to the Dilleniidae, and of the Juglandales to the Rosidae. Affinities of numerous problem taxa, such as the Didymelaceae and Medusagynaceae, are resolved, as are some of the points of disagreement between the Takhtajan and Cronquist arrangements. This analysis also provides the first systematic summary of dicot leaf architectural features and the outlines of a regular systematic method for leaf determination.

Inclusion of a paper dealing with vegetative morphology in a symposium on the Bases of Angiosperm Phylogeny may seem anomalous to many. Vegetative aspects such as branching patterns, phyllotaxy, growth form, leaf outline, and stem, bud, and root features have been extensively described and interpreted functionally and ontogenetically by workers such as Kerner (Kerner & Oliver, 1895), Goebel (1905), Troll (1967), and Radford et al. (1974). A limited systematic value has been recognized for vegetative features, especially within families and genera (see especially Hallé's work on the architecture of trees, Hallé & Oldeman, 1970; Hallé, 1971), and they have been used, usually as adjunct features, in the construction of taxonomic keys. However, no meaningful application has ever been made of vegetative morphology to the systematic consideration of angiosperms at the higher taxonomic levels.

Now our studies of modern and fossil angiosperm leaves indicate that coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships do exist among the leaves of the dicotyledons, and it is in order to elucidate these that we are making the following report. Because

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our experience has been restricted to leaves and because leaves appear to provide a far more abundant and varied set of characters than other vegetative organs, these will be the only features examined in this report.

The study of leaf morphology, particularly in its systematic applications, has been a regrettably neglected area of study by modern botanists. This was due in part to a belief in the plasticity of the leaf under a variety of environmental conditions and selective processes and to their possession of a seemingly bewildering array of features difficult to describe. As with other vegetative characters, some limited use was made of leaves in systematic studies and identifications at the familial and generic levels (especially Lam, 1925; Blackburn, 1952; Harrar & Harrar, 1962; Hutchinson, 1969; Preston, 1961; van Beusekom, 1971) but never at higher ranks.

Paleobotanists, on the other hand, have seldom been reluctant to claim that leaves can serve as the basis for angiosperm identification. A number of paleobotanical workers of the late nineteenth and early twentieth centuries, including von Ettingshausen, Saporta, Lesquereux, Hollick, Knowlton, Berry, and Chaney, based a major portion of their research on the identification of angiosperm leaf impressions. No systematic basis for such identifications was ever developed, and when they are critically examined, they are found to rest on gross morphological similarities in features such as leaf shape, principal vein course or marginal outline, or on superficial comparisons to modern herbarium specimens. The resulting volume of misidentifications is now so great that the validity of almost all paleobotanical identifications based on leaves is open to serious questions (Cronquist, 1968: 39–40; Penny, 1969; Hickey, 1971a; Wolfe, 1972; Hickey, 1973; Dilcher, 1974) and much of the previous work must be restudied. Another result of the “picture matching” (Wolfe, 1972, 1973) of extinct forms with fancied modern descendants is the supposed great antiquity of many angiosperm genera leading to a fixist view of the angiosperm record (Doyle & Hickey, in press). In addition, as Cronquist (1968: 6) notes, matching techniques applied to the fossil record cannot by themselves “provide new or independent information on the evolutionary diversification of a group, or on the transitions between groups; they merely document the existence of a particular group at some time in the past.”

Any attempt to utilize the angiosperm leaf in systematic studies must rest on a careful description of its morphology. The first attempt to codify such a terminology for the description of leaves was that of the Austrian paleobotanist, Constantin von Ettingshausen, especially in his publications dated 1858 and 1861. Although he made no effort to discriminate between features which were of taxonomic value and those which were merely descriptive—a shortcoming hardly surprising in view of the pre-Darwinian mentality still prevailing at that time—he did provide the first logical sequence of terminology and a simple means of analyzing vein pattern by the description of vein courses. However, his system remained largely ignored by students of modern plants after that time. More recently there has been a revival of interest in von Ettingshausen’s system resulting in the publication of two classifications of leaf architecture (Mouton, 1970; Hickey, 1973). Hickey’s system, which considerably augmented the scope

of von Ettingshausen's terminology, attempted to formulate unambiguous and non-overlapping definitions for all terms and to analyze their taxonomic utility. It will be adopted as the terminological base for this paper.

Having developed a terminology capable of describing the variations found in the architecture of angiosperm leaves, the next step was to determine if some systematic variation in leaf features corresponding to the various taxonomic groupings could be ascertained. The fact that such patterns can be discerned even at higher levels and that they can be comprehended most clearly when analyzed in terms of the classification systems for the dicots developed by Takhtajan (1966, 1969) and Cronquist (1968) forms the subject of this report.

The objectives of this paper are thus to:

1. Ascertain the distribution of leaf architectural features in the dicotyledons in terms of the Takhtajan and Cronquist systems of classification;
2. Assemble a plausible systematic ranking and ultimately a phylogeny which incorporates leaf data;
3. Provide the basic data and organization for a synoptic leaf key to the dicots.

The term "leaf architecture" which appears throughout this report will be used in the sense of Hickey (1973) to denote the placement and form of those elements constituting the outward expression of leaf structure, including venation pattern, marginal configuration, leaf shape, and gland position. Architecture in this sense is that aspect of morphology which applies to the spatial configuration and coordination of those elements making up part of a plant without regard to histology, function, origin, or homology.

Finally, it must be stressed that in assembling the systematic survey which follows, evidence from floral morphology, pollen, embryology, and anatomy was evaluated in addition to that of leaves. While establishing the value of leaves as a systematic character, we recognize that they must be considered in conjunction with other morphological features.

LEAF ONTOGENY

Angiosperm leaves arise as lateral primordia left behind by the apical meristem of the plant axis. Development of the mature leaf occurs through the elongation and expansion of this primordium which proceeds in three overlapping phases. These start with apical growth which is followed by marginal expansion and finally by an intercalary phase (Esau, 1965; Kaplan, 1971, 1973; Pray, 1955, 1963). Each of these stages may be variously prolonged or shortened to produce the wide variety of leaf shapes occurring in the angiosperms. Intercalary growth is absent in fern leaves with open dichotomous venation (Pray, 1960, 1962) and at least in the only form with simple reticulate venation which has been studied (Hara, 1964; however, see Pray, 1960, 1962).

At an early stage, the leaf primordium can be divided into two regions, termed the upper leaf zone and the lower leaf zone (Kaplan, 1973). Kaplan (1971, 1973) has demonstrated that unifacial (radial) monocot and dicot leaves undergo a virtually identical ontogeny. In bifacial dicot leaves the lamina develops, in all

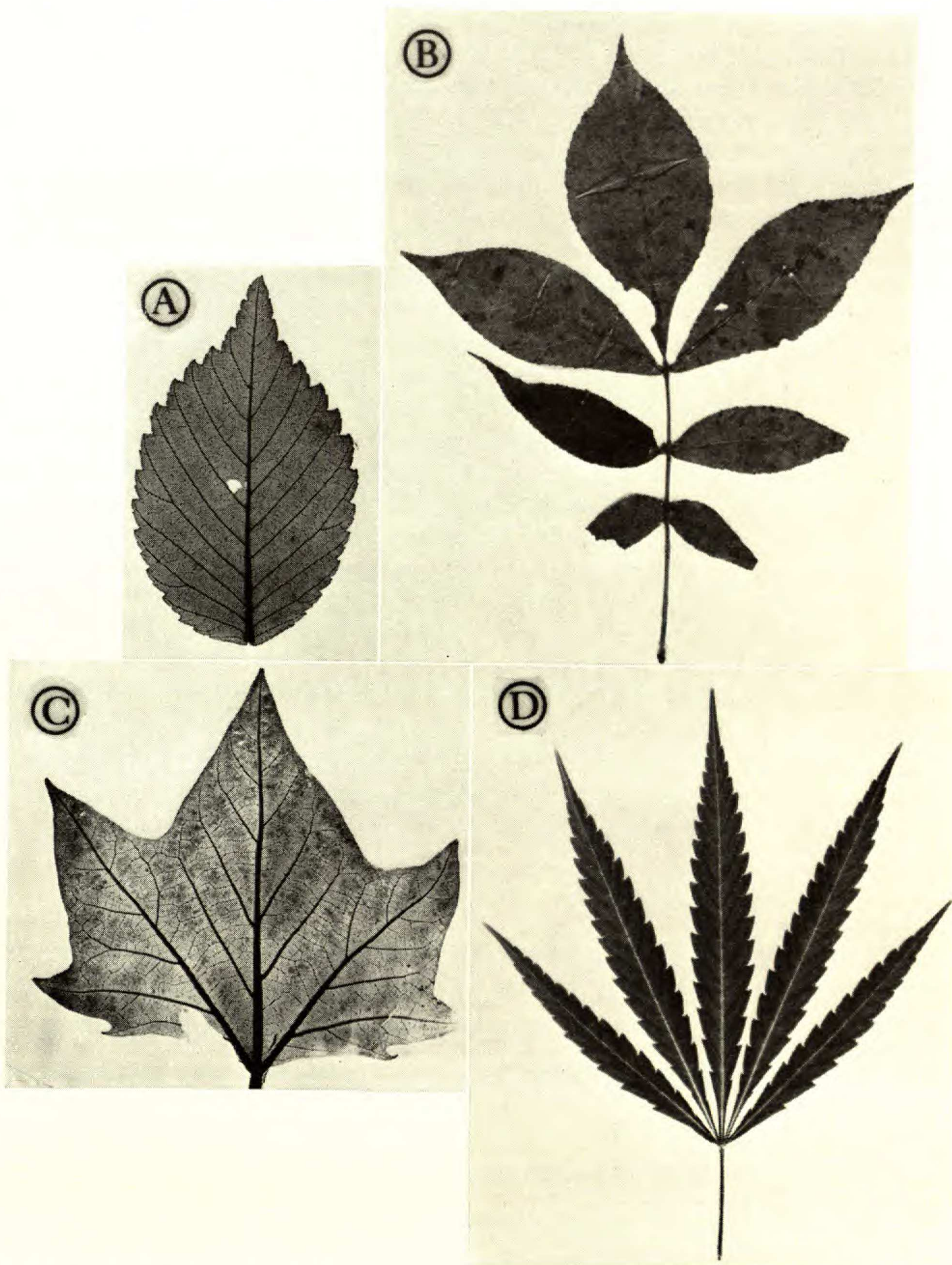


FIGURE 1. Leaf form.—A. Simple, unlobed; *Ulmus floridana* Chapm.; USA: Florida, Standley 12989 (US); $\times 1$.—B. Simple, palmately lobed; *Platanus glabrata* Fernald; Mexico: Coahuila, Pringle 8319 (US); $\times 1$.—C. Pinnately compound; *Carya glabra* Sweet; USA: Louisiana, Stone 437 (US); $\times \frac{1}{2}$.—D. Palmately compound; *Cannabis sativa* L.; USA: Maryland, (USNM Paleobotany Coll. 2013); $\times \frac{1}{2}$. (All photographs by Mr. James P. Ferrigno, Division of Paleobotany, Smithsonian Institution.)

but rare cases, from the upper leaf primordium and the stipules and sheathing leaf base (if any) from the lower leaf primordium. The petiole is intercalated between the two zones as the latest mature structure to appear, and its elongation causes the emergence of the leaf from the bud (Esau, 1965; Kaplan 1971, 1973). In contrast, in all cases where development is known, the blade of bifacial monocot leaves develops from the lower leaf primordium which also gives rise to the petiole, the stipules, and the sheathing base. The upper leaf zone, when present, is a radial projection from the leaf apex called the *Vorläuferspitze* (Kaplan, 1973). This basic difference in leaf development between the monocots and dicots indicates that the blades of each represent convergences in form whose adult morphology cannot be compared (cf. Kaplan, 1973: 446). It was for this reason that the leaf architectural method of Hickey (1973) was restricted to the dicots.

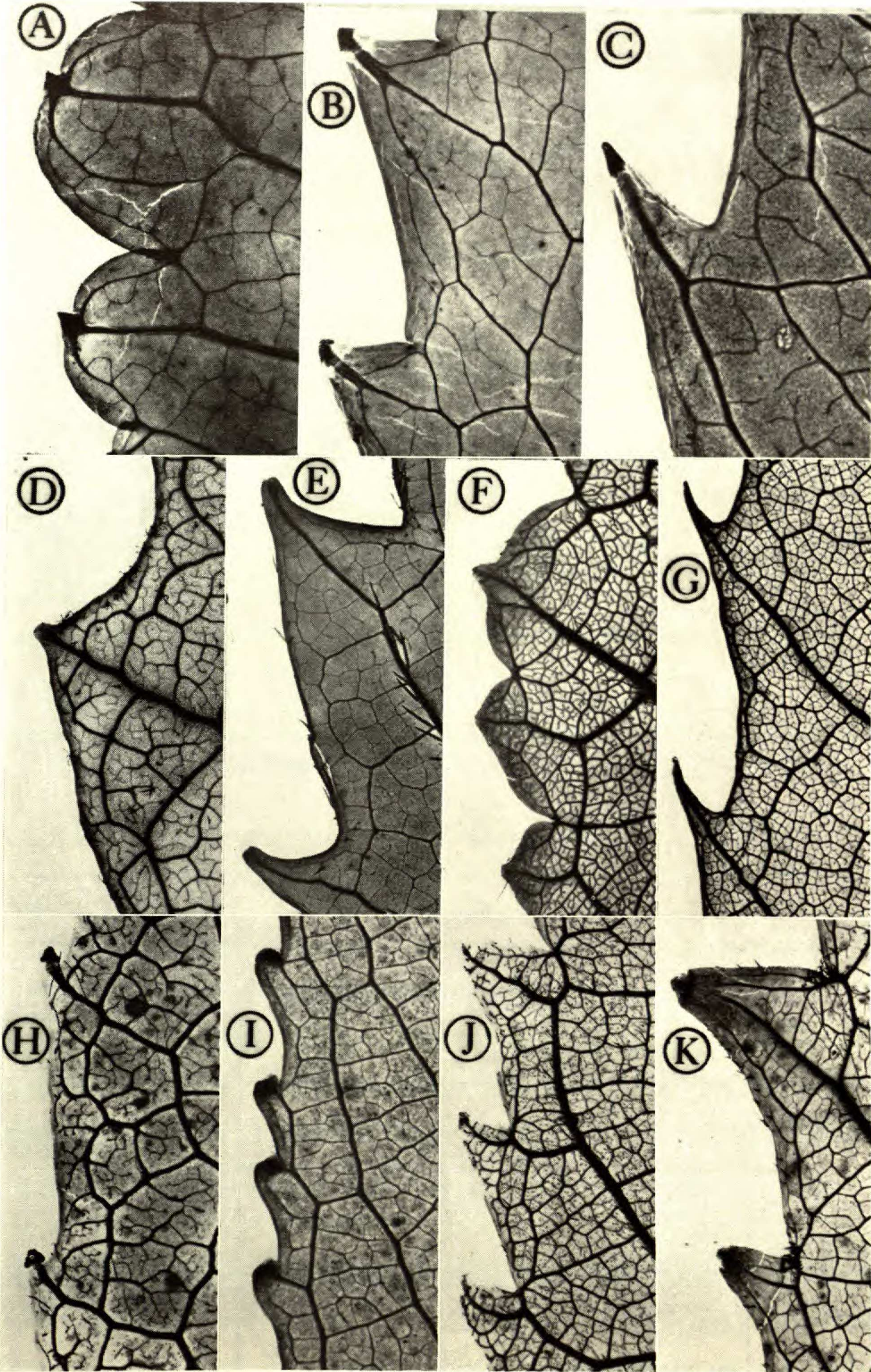
Vein development in pinnate dicot leaves begins with formation of the midvein during apical growth. The secondaries develop progressively outward from the midvein during marginal growth (Esau, 1965; Pray, 1955, 1963; Slade, 1957). The tertiary and higher vein orders develop simultaneously and successively during intercalary growth of leaves having imperfect or well developed areolation (Pray, 1955, 1963; Slade, 1957). Vein endings appear to differentiate progressively from the vascular strands surrounding the areoles (Pray, 1955, 1963; Slade, 1957, 1959). In the one known case of the ontogeny of a leaf with imperfect areolation (*Aucuba* in the Cornaceae) tertiary and higher order vein development is progressive (Pray 1955, 1963). In the monocots and dicots the direction of vein development is acropetal for the primary and secondary veins and basipetal for the higher order vein network (Esau, 1965; Kaplan, 1973).

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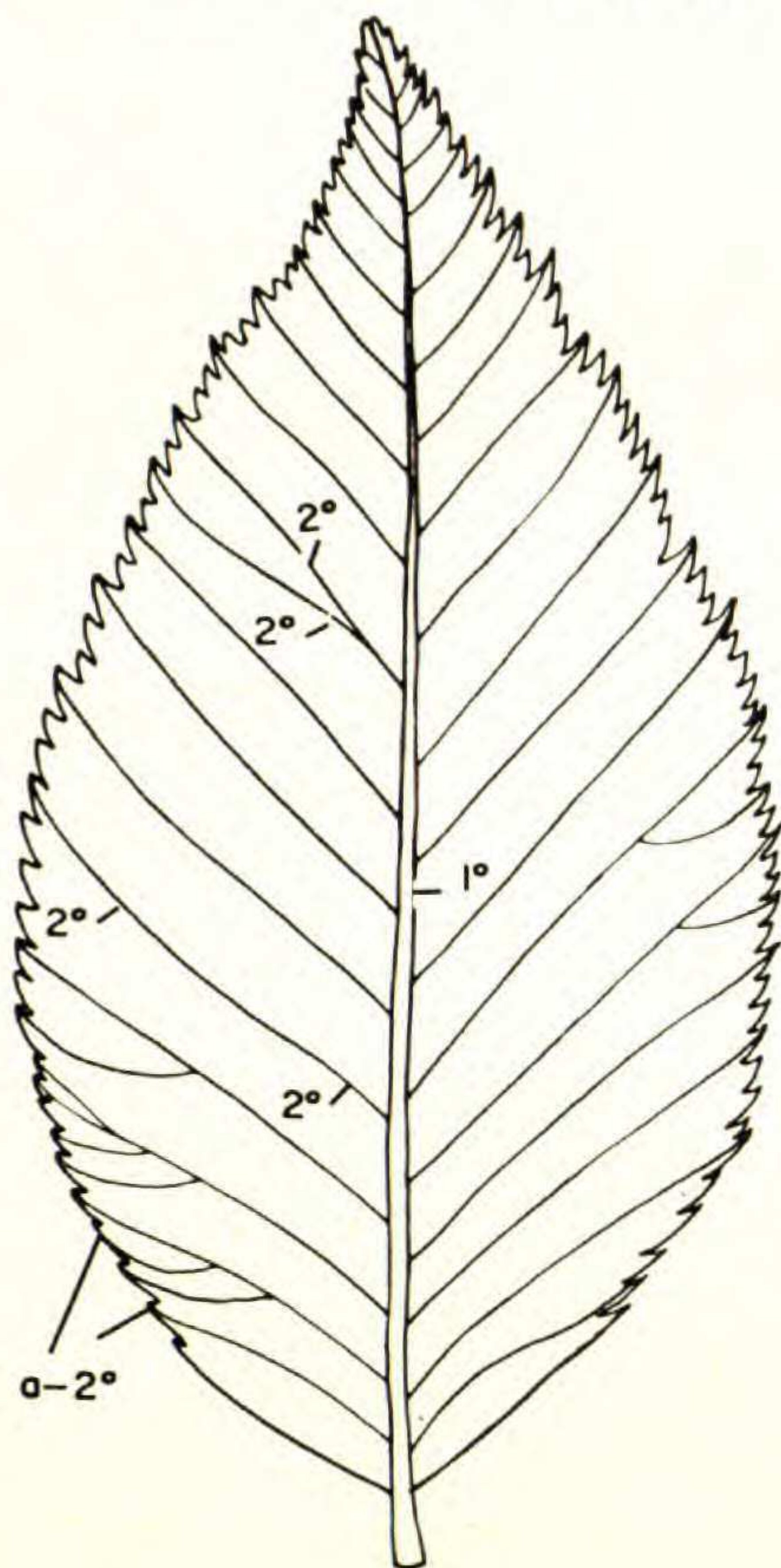
FIGURE 2. Some important tooth types; all $\times 7\frac{1}{2}$.—A. Chloranthoid; *Chloranthus henryi* Hemsl. (Chloranthaceae); China: Yunnan, Henry 9962 (US).—B. Chloranthoid; *Ascarina lucida* Hook. f. (Chloranthaceae); New Zealand: Moehan, Cranwell & Moore s.n. (US).—C. Monimioid; *Atherosperma moschatum* Labill. (Monimiaceae); Australia: Hueber s.n. (USNM Paleobotany Coll. 243).—D. Platanoid; *Fothergilla major* Lodd. (Hamamelidaceae); Ex Biltmore Herbarium 708g (US).—E. Platanoid; *Euptelea polyandra* Sieb. & Zucc. (Eupteleaceae); Japan: Dorsett & Morse 543 (US).—F. Urticoid; *Corylus colurna* L. var. *chinensis* (Franch.) Burkill (Corylaceae); China: Yunnan, Rock 4798 (US).—G. Spinose; *Castanea dentata* (Marsh) Borkh. (Fagaceae); USA: Rhode Island, Bartlett 2681 (US).—H. Theoid; *Hartia sinensis* Dunn (Theaceae); Britain: cultivated, Meyer 6031 (US).—I. Salicoid; *Salix fragilis* L. (Salicaceae); USA: Iowa, Thorne 13312 (US).—J. Cunonioid; *Lamanonia* sp. aff. *speciosa* Camb. (Cunoniaceae); Brazil: São Paulo, Fontella 137 (US).—K. Rosoid; *Ampelopsis brevipedunculata* (Maxim.) Frautrie var. *heterophylla* (Thunb.) Hara (Vitaceae); Phillipines: Luzon, Barnes 20191 (US).

FIGURE 3. Configuration of the principal veins of the leaf and gland position.

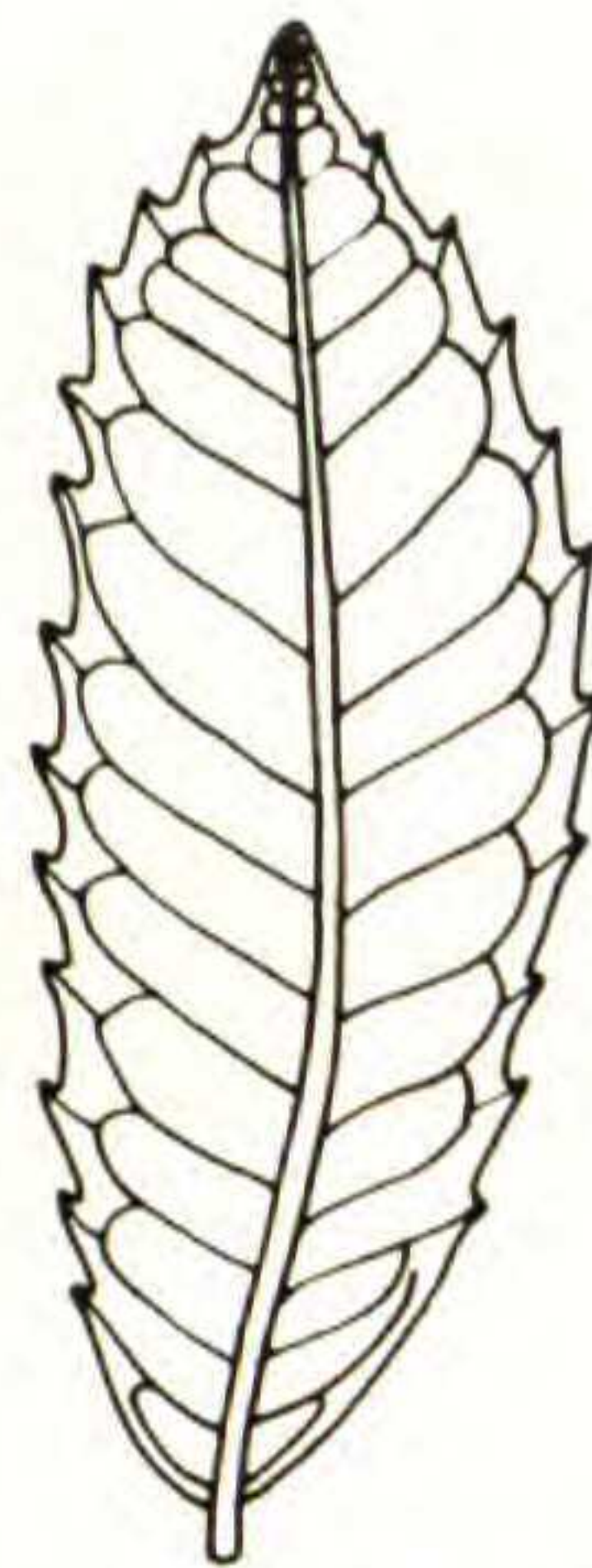
FIGURE 4. Orientation of intercostal venation; all $\times 10$.—A. Random; *Degneria vitiensis* Bailey & A. C. Smith (Degneriaceae); Fiji: Viti Levu, Smith 6301 (US).—B. Admedial; *Trimenia papuana* Ridley (Trimeniaceae); Papua: Brass 23200 (US).—C. Reticulate; *Talauma angatensis* (Blanco) F. Vill. (Magnoliaceae); Philippines: Williams 1354 (US).—D. Reticulate; *Exbucklandia populnea* (R. W. Br. ex Griff.) R. W. Br. (Hamamelidaceae); Sumatra: Bartlett 8007 (US).—E. Transverse, irregularly percurrent; *Canarium pimila* Kon. (Burseraceae); China: Morse 318 (US).—F. Transverse, regularly and strongly percurrent; *Corylus chinensis* Franch. (Corylaceae); China: Hupeh, Wilson 2280 (US).



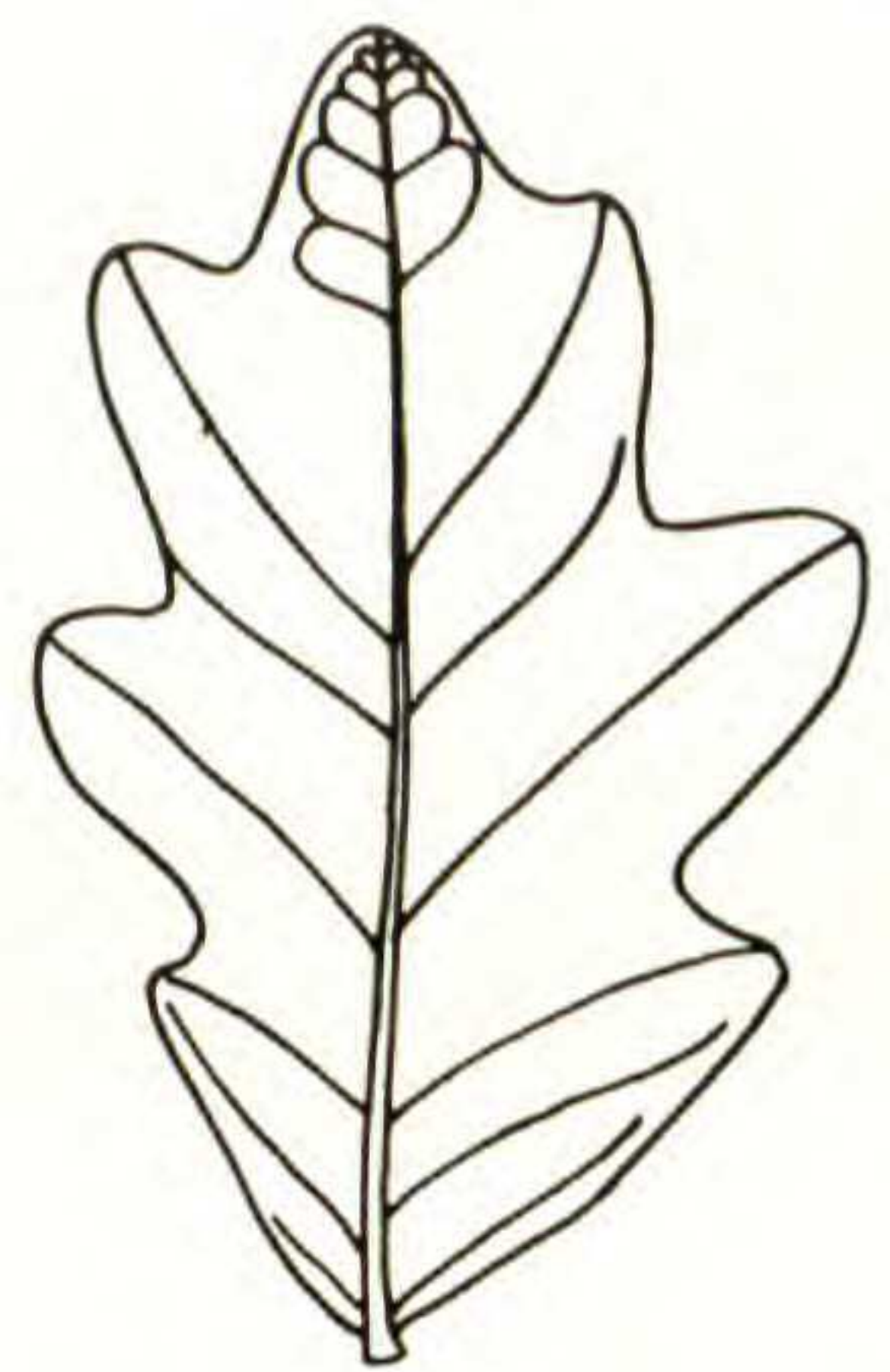
PINNATE VENATION CRASPEDODROMOUS



SIMPLE CRASPEDODROMOUS



SEMICRASPEDODROMOUS CRASPEDODROMOUS



MIXED

CAMPTODROMOUS



BROCHIDODROMOUS



EUCAMPTODROMOUS

"PALMATE" VENATION TYPES

ACTINODROMOUS



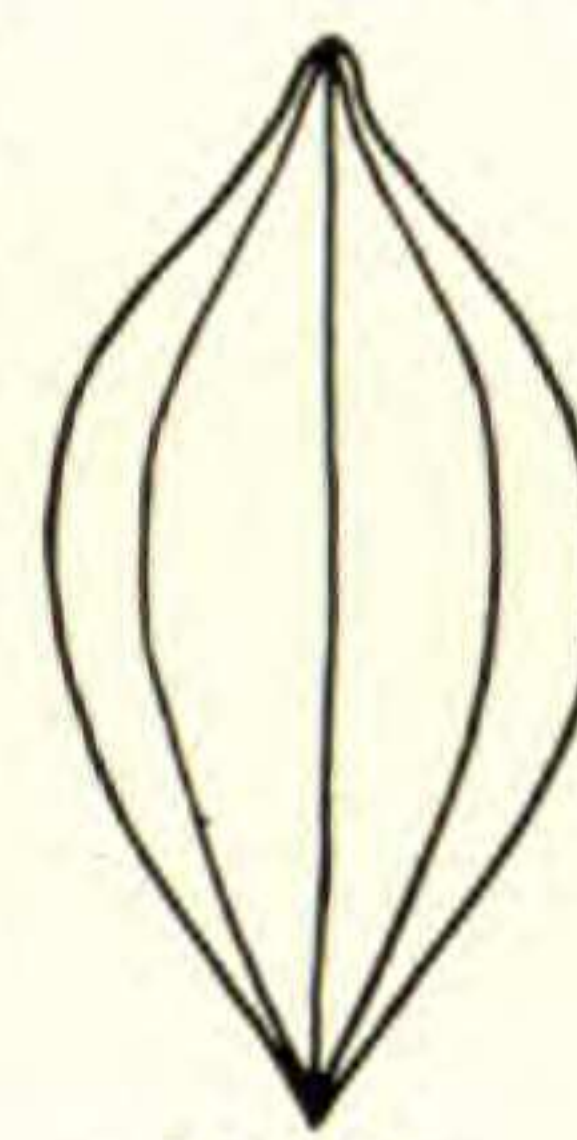
BASAL



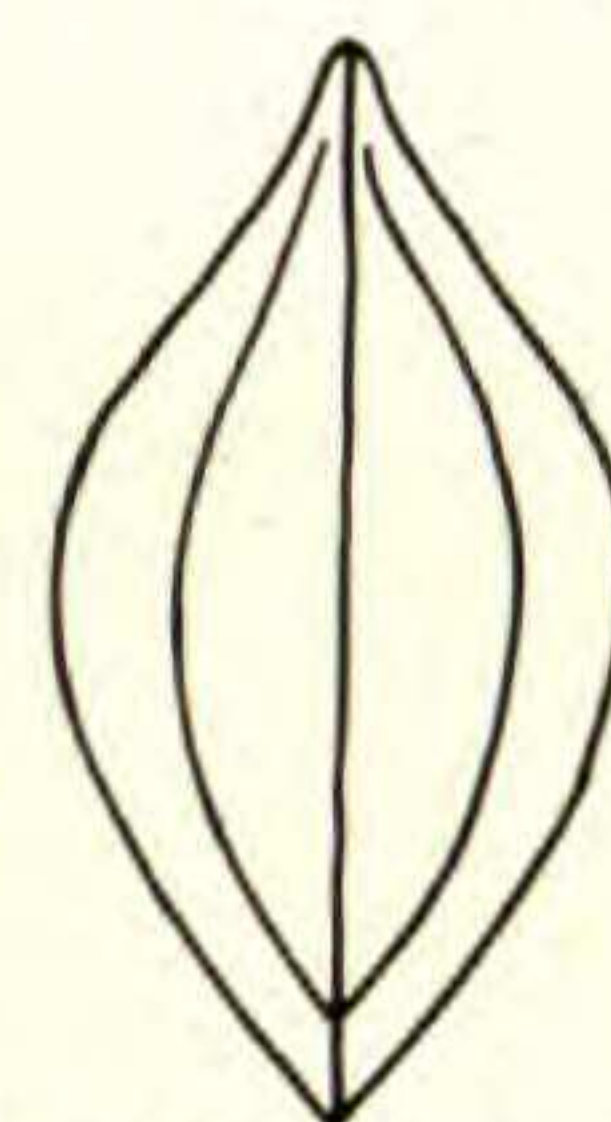
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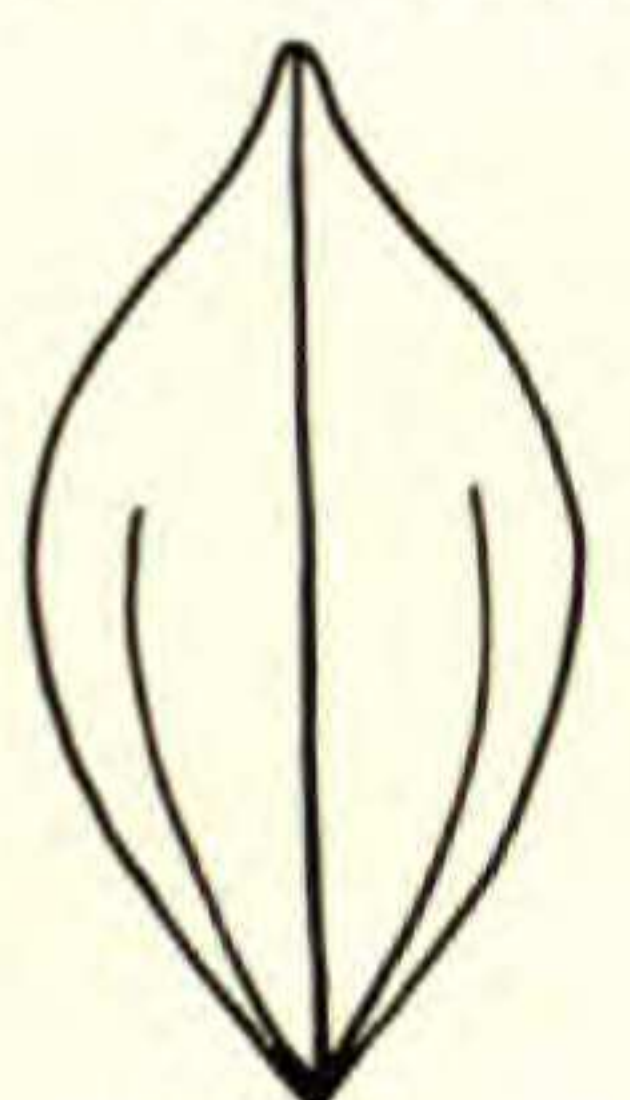
IMPERFECT



BASAL



SUPRABASAL



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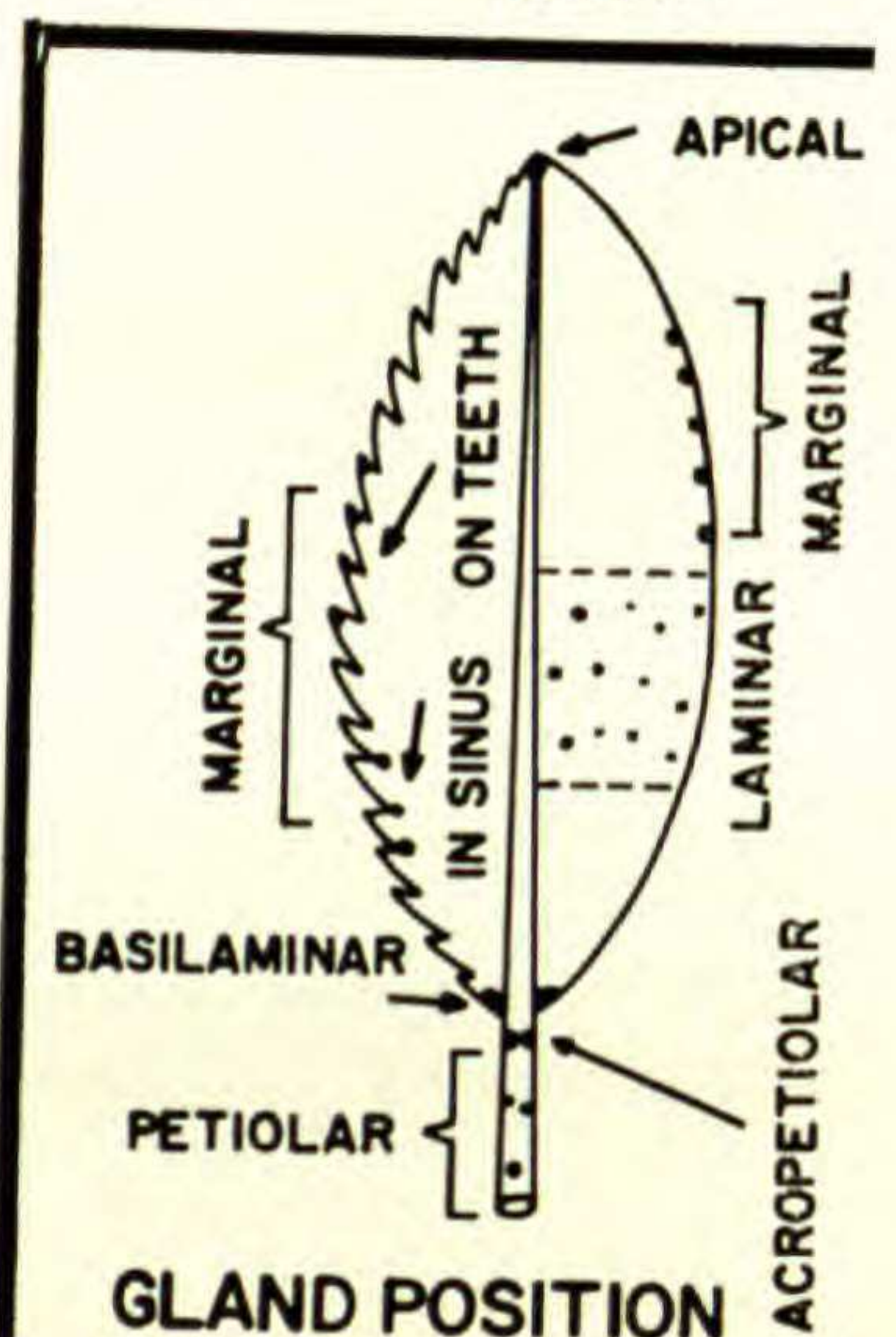
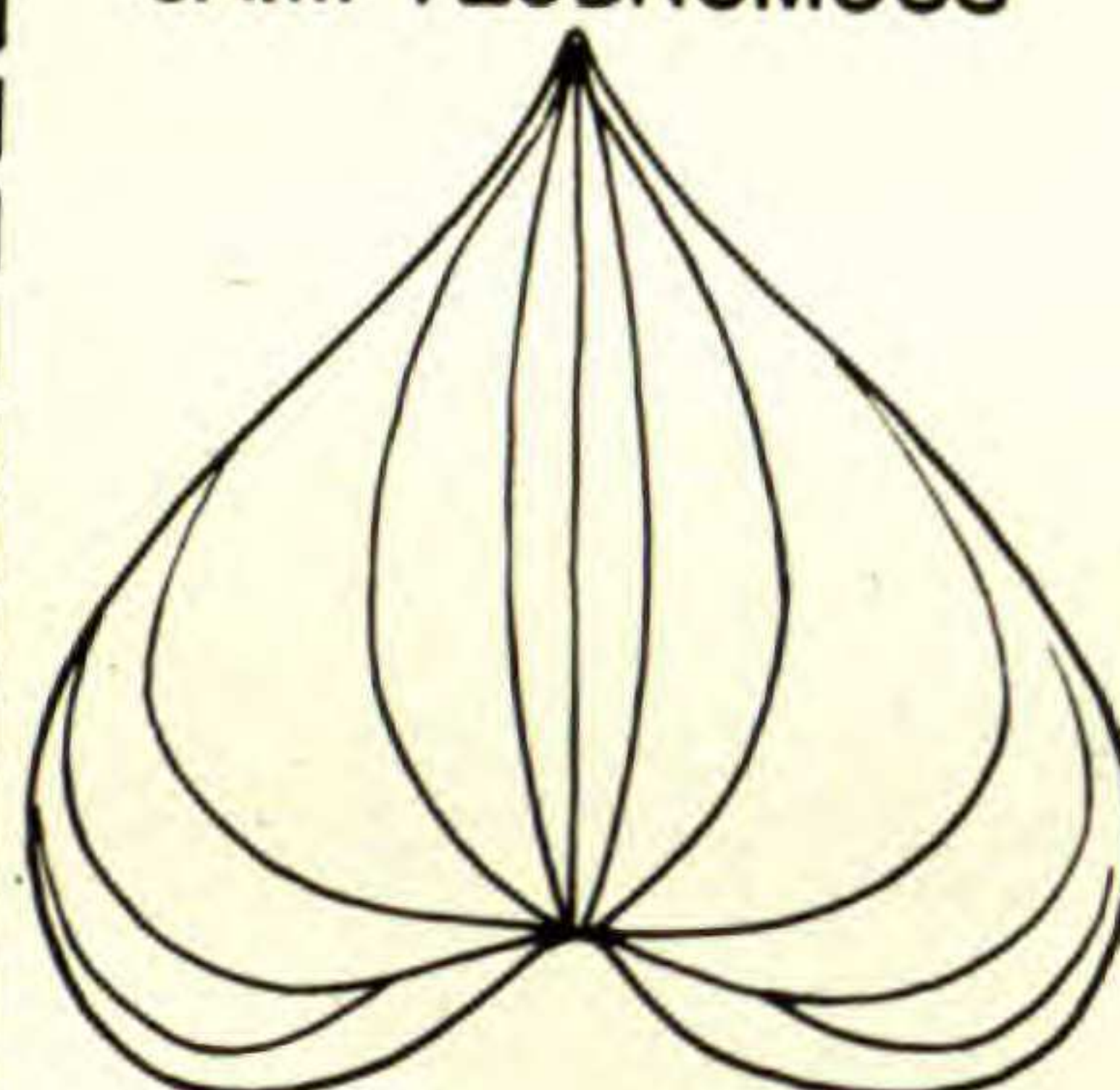


MARGINAL

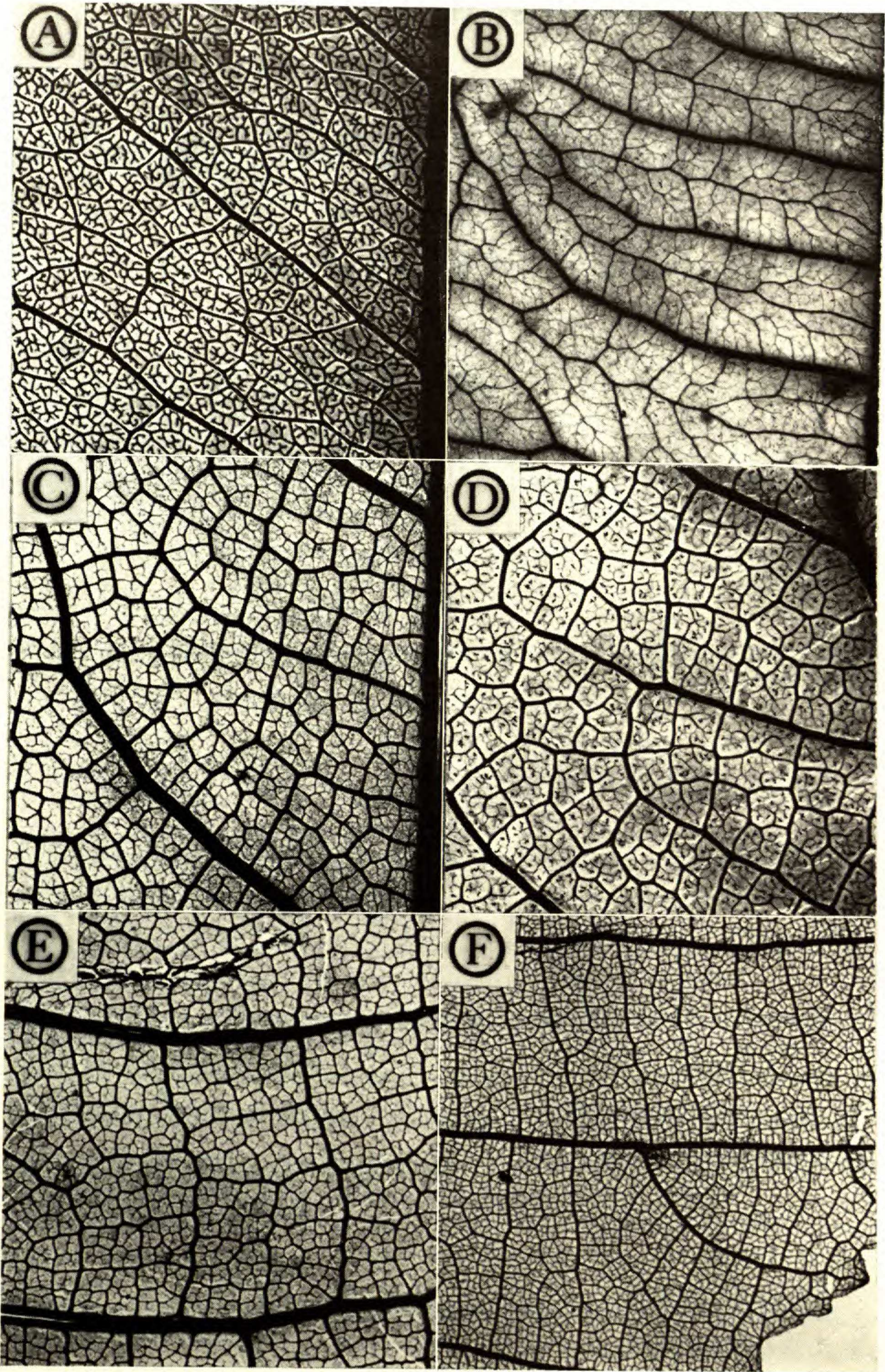


PALINACTINODROMOUS

CAMPYLODROMOUS



GLAND POSITION



FEATURES OF ANGIOSPERM LEAVES

Despite their different modes of ontogeny, both monocot and dicot leaves possess certain common features whereby they can be recognized as angiospermous. None of the characters in the list below are universally present, but the presence of one or more of them is strong evidence of angiospermy. They are:

1. Intercalary growth as the major phase of blade expansion.
2. Stipules. These are frequently absent in the dicots and rare in the monocots where they occur in the Hydrocharitaceae, Butomaceae, Najadaceae, and several other families.
3. Several discrete orders of venation. Almost always three and usually four or more but highly reduced leaves may have fewer than three orders of venation.
4. Freely ending veinlets. Not always present.
5. Vein anastomoses between two or more orders of veins. Not always present but, when so, diagnostic of the angiosperms.

Characteristic features of monocot blades are their development from the lower leaf primordium, a preponderance of parallel venation, and a strong tendency for the longitudinal secondary venation to converge at the leaf apex (Doyle, 1973). Dicot laminae develop from the upper leaf primordium, have a strong tendency toward reticulate venation, and show a predominance of leaves having pinnate venation.

We base our survey of dicot leaf architecture on over ten years of study of the great majority of dicot families from cleared leaves and herbaria collections. Our coverage has been particularly complete in the subclasses Magnoliidae, Ranunculidae, Dilleniidae, Hamamelididae, and Rosidae. At the present time, cleared and stained leaves in the U.S. Geological Survey collection at Menlo Park, California, number approximately 10,500 species and that of the Smithsonian Division of Paleobotany approximately 2,250 species. These specimens were prepared using the method of Foster (1952) modified by Hickey (1973). Taxonomic and collection data on the many tens of thousands of specimens either surveyed or examined in detail in order to complete our review of dicot leaf architectural features are far too voluminous to supply here.

Architectural features of greatest importance in assessing systematic and phylogenetic affinities at the higher taxonomic levels are listed below. These are:

1. Simple versus compound organization (Fig. 1).
2. Entire versus toothed margins.
3. Characteristics of the tooth including shape, characteristics of the apex, occurrence and type of glandular processes, and vein configuration within the tooth (Figs. 2-3).
4. Major vein configuration, e.g., pinnate, actinodromous; secondaries craspedodromous, camptodromous, etc. (Fig. 3).
5. Characteristics of the intercostal venation including its orientation, and the presence and type of intersecondaries (Figs. 4-6).
6. Gland position, including marginal, laminar, acropetiole, etc. (Fig. 3).



FIGURE 5. Leaves showing intersecondary veins between secondaries. In addition, A is "festooned brochidodromous," that is, it has a set of secondary loops outside of the main brochidodromous arch.—A. *Ternstroemia tepazapote* Cham. & Schlecht. (Theaceae); Belize: Gentle 3838 (US).—B. *Pseudoxandra coriacea* R. E. Fries (Annonaceae); Brazil: Terr. Amazonas, Wurdack & Addersley 43492 (US). Both $\times 1$.

These terms and ones related to them will recur frequently in the detailed descriptions and are fully defined by Hickey (1973, in press). Description of tooth types, which proved to be a major systematic tool in this survey, will be a part of the description of the subclass in which they occur. Further definitions of tooth descriptive terms may be consulted in Hickey (in press).

PROCEDURES

In the summaries which follow we will use the classifications of Takhtajan (1966, 1969) and Cronquist (1968) as the systematic framework for presenting our data on leaf architectural variation. We found these systems to yield the most coherent arrangement of foliar features. We supplemented this with data from other systems, particularly from those of Thorne (1968) and Airy Shaw (1966), where we felt that this was warranted. If evidence from foliar morphology indicated that a particular family or order had been misplaced, especially if this was supported by other features, we described it where its foliar features suggested that it fit better. In a number of cases leaf architecture helps to resolve areas of disagreement between Takhtajan and Cronquist, e.g., leaf data support Takhtajan's assignment of the Euphorbiaceae to the subclass Dilleniidae, while Cronquist appears to have been correct in excluding the Lecythidaceae from the subclass Rosidae.

We also tried to establish the "basic" leaf features for each of the taxa from

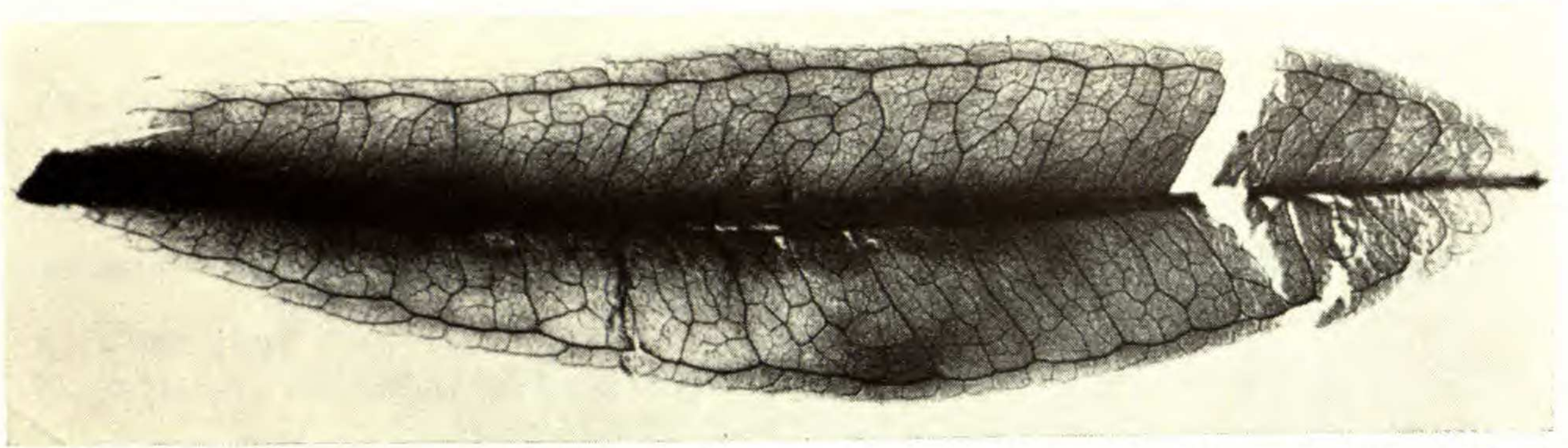


FIGURE 6. Intramarginal vein in *Hibbertia ebracteata* Bur. ex Guillaum. (Dilleniaceae); New Caledonia: M. des Sources, McKee 2097 (US); $\times 1$. Such veins are inferred to form by the fusion and strengthening of the secondary vein segments forming the brochidodromous arch.

subclass through order and in some cases to the level of family. Our concept of basic features are those that serve as the most general types from which all the more specialized types occurring within a taxon could have been derived. These basic characters are not necessarily the most primitive that ever occurred within the taxon. Such features may have been markedly unsuccessful in the long run but were able to give rise to the basic set which then underwent radiation and diversification.

In the following summary of basic characters of the various taxa, especially for the subclasses, we have included only those about which we could make a judgment. Our designation of a character as basic was reached by application of the six criteria listed below, of which only the relatively scanty contribution from the fossil record could be considered as conclusive evidence, rather than merely indicative.

The criteria are:

1. The fossil record.
2. Features possessed by the most primitive living member(s) of a taxon.
3. Features possessed by a number of taxa that are related to the one being analyzed either as ancestors, direct descendants, or as common descendants.
4. Features possessed by the most primitive members of a number of subdivisions of the taxon under examination.
5. The presence, even in only a few forms of a taxon, of a feature considered irreversibly lost, such as a characteristic tooth type.
6. A hypothetical combination of features needed to reconcile a number of trends considered divergent from a common ancestor.

As an example of our reasoning, after applying these criteria to a summary of basic characters in the subclass Ranunculidae, we could reach no judgment as to the status of latex. Thus, mention of this character was excluded from the description of the subclass.

The concept of what constitute the basic features of a taxon has permitted us to assemble the summary which follows. It is organized so that it can be used in a synoptic way to systematically determine the higher level affinities of unknown leaves. This is especially so in the case of the diagrams representing groupings

TABLE 1. Primitive versus advanced features of dicotyledonous leaves. Fossil evidence is available for items 1 through 5 only. (From Doyle & Hickey, in press.)

Primitive	Advanced
1. Leaves simple	1. Leaves compound
2. Pinnate venation	2. Other configurations
3. Secondaries camptodromous	3. Other configurations
4. First rank level of vein organization	4. Higher ranks
5. Margin entire	5. Margin toothed or lobate
6. Stipules present	6. Stipules absent

of leaf characters in the various subclasses where a number of probable convergences in leaf architecture may have been grouped together. This arrangement was maintained because it represents a coherent grouping of characters facilitating leaf identification, and not because it necessarily represents an accurate picture of dicot phylogeny.

Although data from the fossil record are still rare, they did provide some assistance in determining which leaf architectural features are primitive and which are advanced (summarized in Table 1). In certain cases this allowed general trends within subclasses to be established on grounds other than modern comparative morphology. Evidence that items one through five of Table 1 represent primitive character states for dicot leaves is derived from studies of the earliest known fossil angiosperm leaf assemblages which occur in the probable early Aptian Stage of the Cretaceous Period (Doyle & Hickey, in press). These leaves are all simple with pinnate venation and irregularly brochidodromous secondary veins forming a set of loops that do not intersect the leaf margin. These authors (Hickey & Doyle, 1972; Doyle & Hickey, in press) also described a trend in which the earliest angiosperm leaf fossils have all of their vein orders poorly differentiated from one another and are irregular in their courses, manner of branching, and anastomoses. These features are associated with decurrency of secondary veins, irregularly shaped intercostal areas, and often with poor separation of blade and petiole. From this "first rank" stage, Albian-early Cenomanian leaves show a gradual increase in vein differentiation and regularity of course and spacing at progressively higher orders of venation. This pattern coincides with a general trend for increase in leaf rank with supposed phylogenetic advancement in modern leaves found by Hickey (1971b) and was an aid in corroborating our surmises as to advancement at the ordinal and familial levels.

Fossil evidence for point five in Table 1 is somewhat less certain since two rare serrate forms are found even in the lowest level of angiosperm leaf occurrence. However, these fossil leaves are not diverse in tooth shape or form and they occur among a far more diverse and abundant group of entire-margin leaves. In our opinion, these facts argue for the more recent origin of serrate types.

The evolutionary status of stipules is unclear since fossil evidence is lacking and evidence from comparative morphology is subject to conflicting interpretations. However, their presence in both monocots and dicots (Eames, 1961; Sinnott & Bailey, 1914), their common association with the more primitive dicot

families, and their generally vestigial nature lead us to the conclusion that they are in the process of phylogenetic reduction (Cronquist, 1968) and seem to indicate that stipules are primitive. Controversy over stipules necessarily involves the question of which type of nodal anatomy is primitive, inasmuch as stipules are found in association with tri- or multilacunar nodes (Sinnott & Bailey, 1914), whereas in their rare occurrences in unilacunar families, they are mainly scarious or minute.

Rather than reviving the controversy, we simply adopted as a general operating principle the condition that we would derive no stipulate, multilacunar group from an exstipulate taxon. We felt that the status of unilacunar stipulate leaves was unclear, as in the case of a stipulate species of *Garcinia* in the typically exstipulate family Guttiferae. Since all the characters of the inflorescence and foliar morphology of *Garcinia* are advanced, stipules may represent either a survival or a secondary acquisition.

SUMMARY OF LEAF FEATURES

In the following sections descriptions of dicot leaf architecture are carried to the level of orders where information is available. Important leaf trends or specializations manifested by particular families are also included, but an overall survey at familial level is beyond the scope of this paper and will be dealt with in a later publication.

Again it must be emphasized that the basic framework of ordinal relationships within and to the seven dicot subclasses is that of Takhtajan and Cronquist, with modifications as indicated from leaf architecture and other references. The listing of orders and especially the charts of leaf architectural relationships thus developed are not meant to be interpreted in a phylogenetic sense but to serve as visual schemes which allow an initial approach to be made in placing an unidentified leaf in a subclass and order. Despite the fact that evidence from as many organs as possible was evaluated, in addition to the Takhtajan and Cronquist systems, in arriving at these groupings, there is little doubt that some of the leaf architectural relationships we recognize are artificial. However, as the diagrams are meant to illustrate these leaf architectural relationships, we feel that they are satisfactory.

For purposes of comparison, Takhtajan's (1969) numbers for the orders have been retained throughout this summary, even where leaf architectural or other data indicate a change in the placement of the orders.

The following synoptic key to the subclasses of the dicotyledons is designed as a conceptual aid in visualizing their leaf features and not primarily as an identification tool. The entries are necessarily generalized and exceptions have been minimized or disregarded.

LEAF KEY TO THE DICOT SUBCLASSES

- a. Leaf basically simple or, if compound, then palmately compound; latex occasionally present.
- b. Margin basically entire.
- c. Third and higher order venation mostly well developed and staining well with Safranin O; leaves of normal texture.

- d. Primary venation basically pinnate, becoming perfect acrodromous, actinodromous, or campylodromous; secondaries festooned brochidodromous (i.e., looping in several orders, Fig. 5) to simple brochidodromous, to eucamptodromous; intramarginal veins absent (Fig. 6); intercostal venation random, reticulate, or percurrent; latex present only in the aquatic order Nymphaeales A. MAGNOLIIDAE (in part)
- dd. Primary venation basically pinnate, becoming imperfect acrodromous; secondaries basically strongly brochidodromous and often forming an intramarginal vein (Fig. 6); intercostal venation often oriented parallel to the secondaries; latex common G(I). DILLENIID-LEAFED ASTERIDAE
- cc. Third and higher order venation mostly poorly developed and staining poorly with Safranin O; leaf texture often thick, fleshy, or mealy .. D. CARYOPHYLLIDAE
- bb. Margin basically toothed.
 - e. Leaves basically pinnately veined with secondaries not congested toward the base; lamina never palmately compound.
 - f. Leaf margin with Chloranthoid or Monimioid Teeth (Fig. 2); intramarginal vein lacking; latex absent A. MAGNOLIIDAE (in part)
 - ff. Leaf margin with Dillenioid, Theoid, or Spinose Teeth (Fig. 2); intramarginal vein sometimes present; latex widespread E. PINNATE DILLENIIDAE
 - ee. Leaves basically palmately veined or, if pinnate, with secondaries congested toward the leaf base; lamina sometimes palmately compound.
 - g. Leaf margin with Chloranthoid, Platanoid, or Urticoid Teeth (Fig. 2) or their presumed derivatives; primary venation either actinodromous or palinactinodromous; tertiaries percurrent but not tending to become concentrically oriented with respect to the top of the petiole; latex absent C. HAMAMELIDIDAE
 - gg. Leaf margin with Theoid Teeth or their presumed derivatives (Figs. 2, 15); primary venation perfect or imperfect actinodromous or its derivatives; tertiaries transverse, tending to become concentrically oriented with respect to the top of the petiole; latex often present E. PALMATE DILLENIIDAE
- aa. Leaf basically pinnately compound; latex absent.
 - h. Leaf form basically ternately pinnately compound, with ternately forking primary and secondary venation; or if simple, then with a fimbrial vein; leaf margin with Chloranthoid Teeth or their derivatives B. RANUNCULIDAE
 - hh. Leaf form basically pinnately compound, not ternate, also palmate or palmately lobed by compression of the rachis; if simple, without a fimbrial vein; leaf margin with Cunonioid Teeth (Fig. 2) or their derivatives F. ROSIDAE and G(II). ROSID-LEAFED ASTERIDAE

SUMMARY OF DICOT LEAF FEATURES

SUBCLASS A. MAGNOLIIDAE

Leaves simple; margin basically entire; venation pinnate; secondary veins basically festooned brochidodromous (i.e., with several orders of marginal loops, Fig. 5A); intersecondary veins common; tertiary venation grading from random to reticulate and transverse; glands none; stipulate; latex present only in the Nymphaeales (Fig. 7).

Trends: 1. Breakdown of primitively pinnate venation (Doyle & Hickey, in press) to acrodromous in the Laurales and Piperales, campylodromous in the Aristolochiales, and actinodromous in the Nelumbonales. 2. Teeth in the Laurales, Chloranthaceae, and Illiciales. 3. Loss of intersecondary veins. 4. Transverse intercostal venation. 5. Loss of stipules.

The Illiciales are brought within this subclass on the basis of their nodes, simple leaves, and brochidodromous venation. These characteristics make the order anomalous for the Ranunculidae, in which it was placed by Takhtajan. In

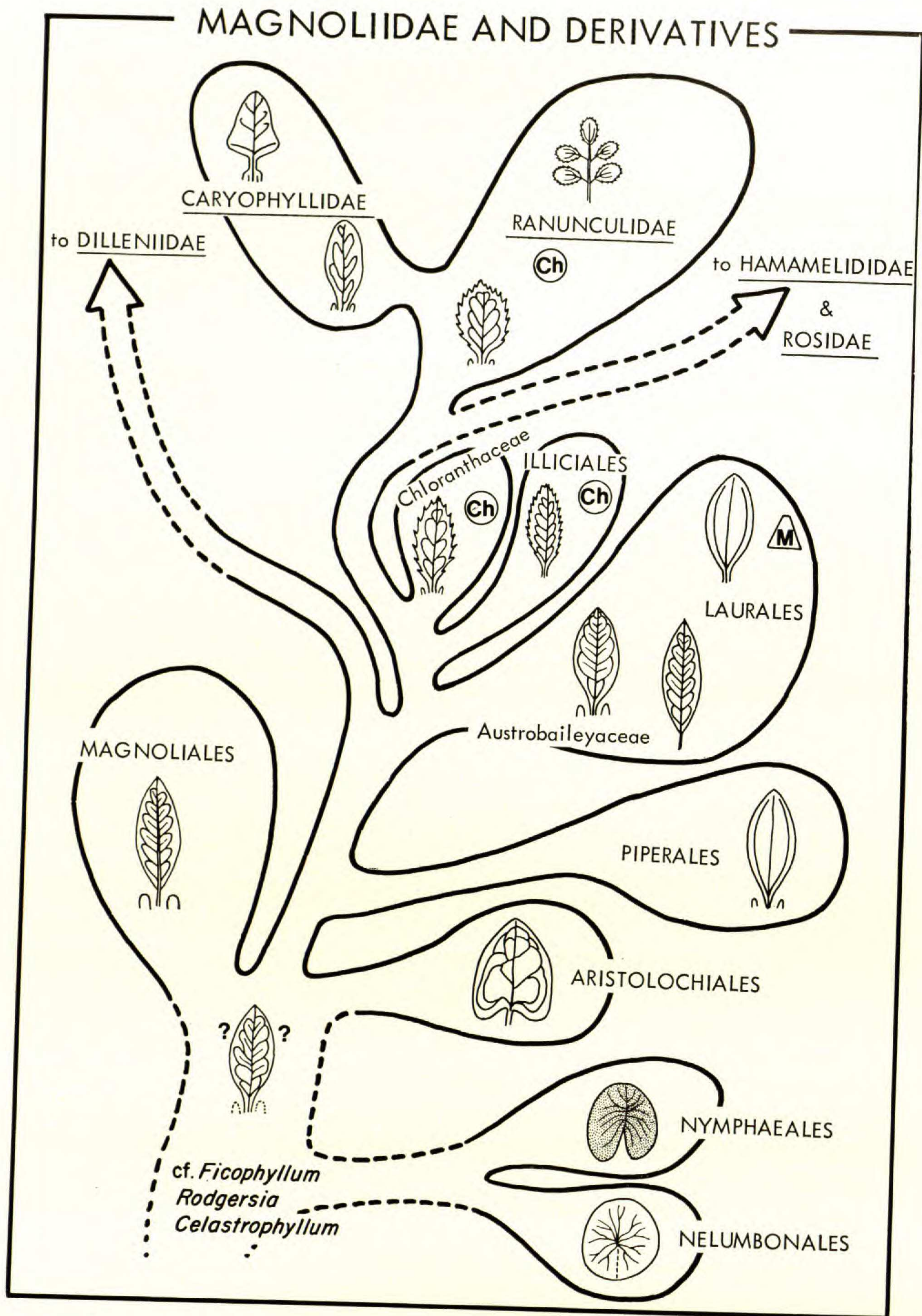


FIGURE 7. Leaf affinities in the Magnoliidae and derivatives. In this and the following affinity diagrams, positions represent morphological relationships which may or may not have a phylogenetic basis. The Takhtajan subclasses are underlined; taxa having latex are indicated by stippled leaves. Taxa having toothed leaves and the type of tooth are indicated by the

addition, the Nelumbonales are also brought within the subclass as an order more advanced than, but related to, the Nymphaeales. Inclusion of these forms with tricolpate pollen within the subclass assumes that this condition has arisen in separate lines of the dicots (see Muller, 1970: fig. 1; Walker, 1974).

Order 1. Magnoliales

Leaves simple; margin entire; venation pinnate; secondary veins festooned brochidodromous; intersecondary veins present; tertiary venation random, reticulate to transverse; stipulate.

Trends: 1. To eucamptodromy. 2. Disorganized to regular venation. 3. Loss of stipules in all families but the Magnoliaceae.

Order 2. Laurales (excluding Chloranthaceae)

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous with basal ones originating at a lower angle than those above; intersecondary veins common; tertiary venation reticulate to transverse; stipulate.

Trends: 1. Development of the Monimiod Tooth (Fig. 8 and defined below) having an unbraced medial vein; found in the Monimiaceae and the Trimeniaceae. 2. Secondaries originating at a uniform angle in the Monimiaceae, most Trimeniaceae, Lactoridaceae, Calycanthaceae, and Idiospermaceae. 3. To acrodromous venation in Amborellaceae, Hernandiaceae, and some Lauraceae. 4. To exstipulate in all families but Austrobaileyaceae and Lactoridaceae.

Family 15. Chloranthaceae

Leaves simple; margin with Chloranthoid Teeth having a medial vein "braced" by two prominent laterals which join it (Fig. 8); venation pinnate; secondary veins basically semicraspedodromous; tertiary venation random, reticulate to weakly transverse; venation staining poorly in Safranin O; stipulate.

Howard (1970, 1974) has shown that Swamy (1953) was incorrect in classifying the nodes of *Sarcandra* and *Chloranthus* as "modified unilacunar." In reality, leaves in these genera each have three gaps, with the two lateral gaps shared with the opposite leaf of the pair. The trace arising from these lateral gaps is also shared or "split," forking above its origin and sending a girdling bundle through the cortex into the marginal portion of both leaves. Howard classified these "split lateral nodes" as a new type but showed their close association with families and genera having the trilacunar condition. We think that this gap clearly arises from the standard trilacunar type in certain plants having opposite leaves and should most appropriately be considered as a modification of that type, termed perhaps the "shared trilacunar gap." Presence of these modified trilacunar gaps in the Chloranthaceae make it anomalous for the Laurales. In addition, if the Chloranthoid Tooth, which the family shares with the trilacunar ranunculids and Trochodendrales and with the unilacunar Illiciales,

←

symbol shape and the letter within the symbol. M = Monimiod; Ch = Chloranthoid. Possible affinity with the Lower Cretaceous fossil genera *Ficophyllum*, *Rodgersia*, and *Celastrophyllum* is indicated by question marks.

originated only once, and if the trend to unilacunar nodes is irreversible, then Chloranthaceae should be derived from trilacunar stock having Chloranthoid Teeth and would not be closely related to the basically entire-margined Laurales, where an entirely different tooth type—the Monimioid—developed in two families.

Order 7. Illiciales

Leaves simple; margin with Chloranthoid Teeth; venation pinnate; secondary veins brochidodromous; tertiary venation random to reticulate or transverse; staining poorly in Safranin O; glands lacking; exstipulate.

Trends: Loss of teeth in the Illiciaceae except in *Illicium anisatum*.

Order 3. Piperales

Leaves simple; margin entire; venation acrodromous; stipulate. Highly disorganized venation is found in the herbaceous family Saururaceae.

Order 4. Aristolochiales

Leaves simple; margin entire; venation acrodromous; exstipulate.

Trends: The acrodromous venation of *Saruma* and *Asarum* becomes campylo-dromous in *Aristolochia* with a corresponding increase in vein regularity and leaf rank.

Order 6. Nymphaeales

Leaves simple, deeply lobed at the base with the margin reaching the centrally placed petiolar attachment; margin entire; venation essentially pinnate with the secondary veins strengthened and radiating actinodromously; latex present.

Order 8. Nelumbonales

Leaves simple, truly peltate by apparent fusion of the basal lobes along a line of suture; margin entire; venation truly actinodromous with numerous primaries; latex absent.

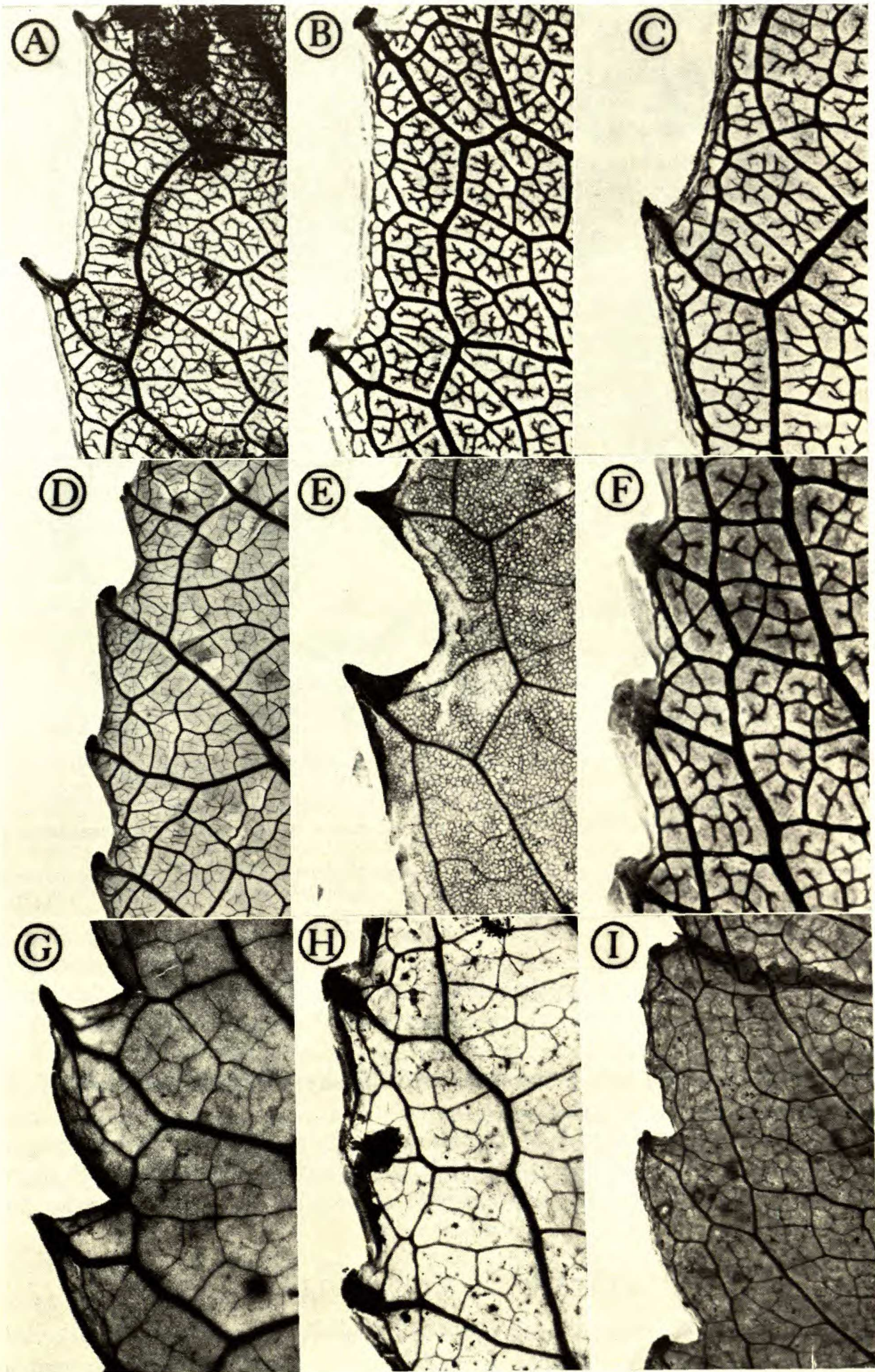
Despite its tricolpate pollen, this order is placed after its apparent nearest relative in the Magnoliales rather than in the Ranunculidae.

Magnoliid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 8)—Chloranthaceae, Illiciales. Glandular; with a clear, non-deciduous (i.e., papillate) swollen cap, shape variable, acumi-

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FIGURE 8. Tooth types and their variation in the Magnoliidae; all $\times 7\frac{1}{2}$.—A–D. Monimioid.—A. *Mollinedia elegans* Tul. (Monimiaceae); Brazil: São Paulo, *Hancho* 2067 (US).—B. *Macropeplus ligustrinus* (Tul.) Perk. (Monimiaceae); Brazil: Rio de Janeiro, *Glaziou* 11991 (US).—C. *Hedycarya arborea* Forst. (Monimiaceae); New Zealand: Bay of Islands, *Wilkes s.n.* (US).—D. *Trimenia* sp. (Trimeniaceae); Africa: *Mundt & Marne s.n.* (US).—E–I. Chloranthoid; all Chloranthaceae.—E. *Sarcandra glabra* (Thunb.) Nakai; Okinawa: *Conores* 1158 (US).—F. *Hedyosmum* cf. *glaucum* Solms; Peru: Huambos, *Souksep* 4472 (US).—G. *Chloranthus serratus* Roem. & Schultz; Japan: Feyiyama, *Dorsett & Morse* 503 (US).—H. *Chloranthus officinalis* Blume; Thailand: Nan Province, *Walker* 7994 (US).—I. *Hedyosmum artocarpus* Solms.; Mexico: Cuernavaca, *Pringle s.n.* (US).



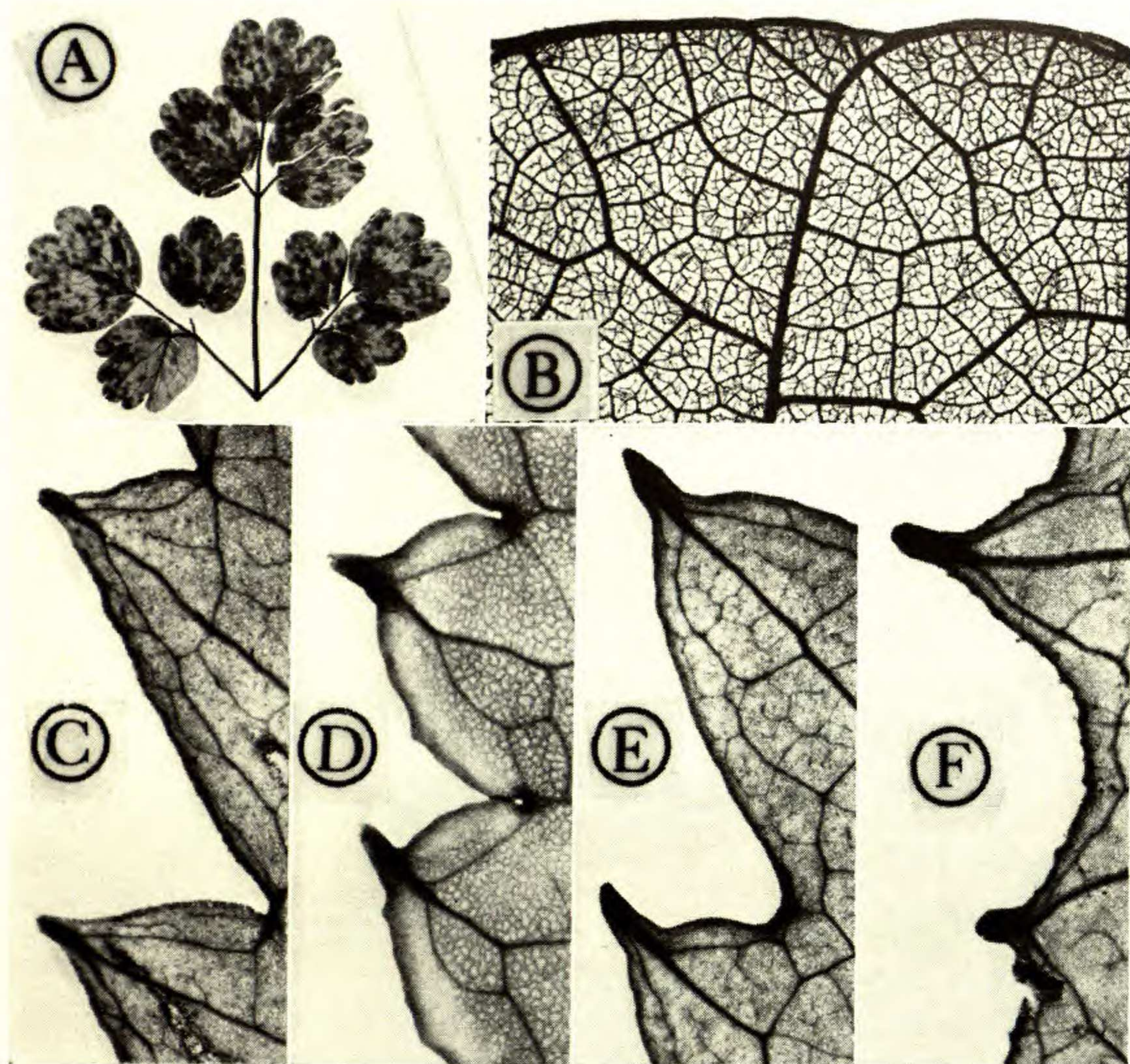


FIGURE 9. Leaf features of the Ranunculidae.—A. Portion of a ternate pinnately compound leaf; *Thalictrum dioicum* L. (Ranunculaceae); USA: Michigan, *Chandler s.n.* (US); $\times 1$.—B. Fimbrial vein; *Cyclea polypetala* Dunn (Menispermaceae); China: *Henry 11979A* (US); $\times 5$.—C–F. Chloranthoid Teeth; all $\times 10$.—C. *Actaea pachypoda* Ell. (Ranunculaceae); USA: Virginia, *Palmer & King 76* (US).—D. *Beesia calthaefolia* (Maxim.) Ulbr. (Ranunculaceae); China: Hupeh, *Wilson 1292* (US).—E. *Podophyllum emodi* Wall. (Podophyllaceae); Pakistan: Punjab Province, *Rodin 5353* (US).—F. *Diphyllia grayi* F. Schmidt (Podophyllaceae); Japan: Shinano, *Collector Unknown* (US 205563).

nate-convex is common, acuminate-acuminate and concave-acuminate also occur. Venation with a medial secondary or tertiary vein accompanied by two prominent, converging, higher order lateral veins which also enter the tooth apex or fuse with the medial vein below the apex. Occasionally, as in *Ascarina*, one of the converging laterals is suppressed.

2. *Monimioid*—M (Figs. 2, 8)—Monimiaceae, Trimeniaceae. With an opaque, non-deciduous glandular cap (i.e., cassidate) having an acute apex; tooth shape generally acuminate-convex; venation with a secondary or tertiary entering the tooth medially and not joined by lateral veins.

SUBCLASS B. RANUNCULIDAE

Leaves basically pinnately compound by ternate forking of the rachis (Fig. 9); margin with Chloranthoid Teeth; venation pinnate, forking ternately; secondary

veins craspedodromous; tertiary venation random, reticulate, transverse; glands none; stipulate (Fig. 7).

Trends: 1. To simple leaves in the Ranunculales. 2. Exstipulate in all but a few Ranunculaceae.

Order 9. Ranunculales

Leaves basically pinnately compound by ternate forking of the rachis; margin with Chloranthoid Teeth; venation craspedodromous with opposite secondaries; stipulate; latex absent.

Trends: 1. Leaves pinnately compound, as in some Lardizabalaceae, Sargentodoxaceae, and many Ranunculaceae, with a trend toward compression of the rachis occurring in the Glaucidiaceae-Hydrastidaceae line and in some Berberidaceae. 2. Leaves palmately compound in some Lardizabalaceae. 3. Leaves bipinnately compound in Nandinaceae. 4. Leaves basically simple in Menispermaceae (but a few advanced types ternately compound!) and Sabiaceae (excluding Meliosmaceae), both with a distinctive fimbrial vein, and in Circaeasteraceae. 5. Actinodromous venation developing in several lines of Menispermaceae, coupled with extension of the secondary veins to the fimbrial vein.

Order 10. Papaverales

Leaves basically pinnately compound; margin toothed, teeth of specialized types including Spinose; exstipulate; latex present.

Ranunculid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 9)—Ranunculaceae, Glaucidiaceae, Hydrastidaceae, Podophyllaceae. Described under the Magnoliidae.

2. *Spinose*—Sp (Fig. 2)—Berberidaceae, Papaveraceae. Medial vein emerging as a spine.

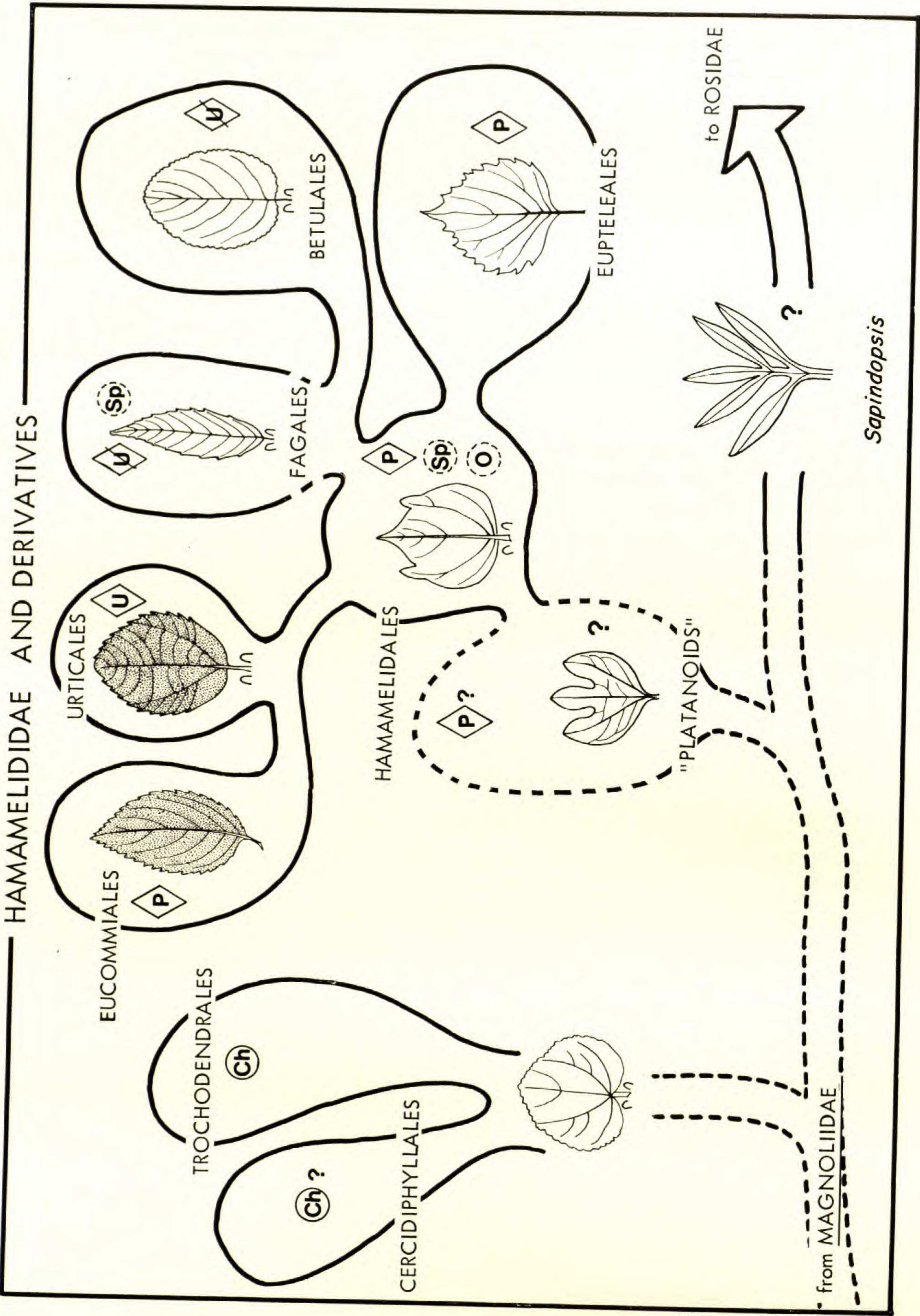
SUBCLASS C. HAMAMELIDIDAE

Leaves simple; margin basically toothed; venation actinodromous; secondary veins brochidodromous; tertiary venation transverse; glands lacking; stipulate (Fig. 10).

Trends: 1. Unlobed palmately veined leaves with incurving primaries in the Trochodendrales, Cercidiphyllales, and some of the Hamamelidales. 2. Palmately lobed leaves in the Platanaceae and Hamamelidaceae. 3. Pinnate venation by suppression of the lateral primaries in Trochodendraceae, some Hamamelidaceae, some Urticales, Fagales, and Myricales. Basally congested secondary veins occurring in these orders are inferred to result from this suppression. 4. Tertiary venation becoming closely spaced and rigidly transverse in the more advanced orders.

Order 12. Trochodendrales

Leaves simple; margin with Chloranthoid Teeth; venation actinodromous; intercostal venation transverse; glands lacking; stipulate.



Trend: Becoming exstipulate and pinnately veined in Trochodendraceae but with the secondary veins congested toward the leaf base.

Order 13. Cercidiphyllales

Leaves simple; margin with convex-convex crenations having a medial vein terminating at the apex and with converging higher order lateral veins (Fig. 11). These teeth possibly represent modified Chloranthoid Teeth. Primary venation inwardly curving actinodromous; secondary veins brochidodromous; stipulate.

Both this and the preceding order with their unlobed leaves and Chloranthoid Teeth possibly derive from a different ancestor than the other Hamamelididae and may not be directly related to lines having had their origins in the lobate "Platanoid" stage (see Fig. 10 and Hamamelidales, below).

Order 14. Eupteleales

Leaves simple; margin with Platanoid Teeth (Figs. 2, 11); venation pinnate; secondary veins craspedodromous and congested toward the leaf base, possibly indicating an actinodromous origin; tertiary venation transverse; exstipulate.

Order 15. Didymelales

To the Dilleniidae; cf. Wolfe (1973).

Order 16. Hamamelidales

Leaves simple, palmately lobed; margin with Platanoid Teeth; venation actinodromous; secondary veins brochidodromous; intercostal venation transverse; stipulate.

Trends: 1. A line of middle and Late Cretaceous leaves termed the "Platanoids" are tentatively regarded as possible early members of the trend toward the hamamelid line (Doyle & Hickey, in press). These are simple palmately lobed leaves with entire margins, palinactinodromous primary veins, and intercostal venation which shows an increase in regularity from random to rigidly percurrent in progressively younger occurrences (Fig. 10). 2. In the fossil record of the Late Cretaceous and Early Tertiary a highly diverse group of probable hamamelids occurred including palmately lobed leaves (*Pseudoaspido-phyllum*), secondarily simple and peltate types (*Protophyllum*), and a palmately trifoliolately compound type ("*Cissus*" *marginata*). The modern family Platanaceae is probably a relict of this radiation. 3. Extreme reduction of the blade in Myrothamnaceae. 4. To specialized non-glandular teeth with convergent higher order lateral veins such as the Spinose type (*Sinowilsonia* and *Corylopsis*) where the medial vein projects beyond the tooth apex; or in *Altingia* where the

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FIGURE 10. Leaf affinities of the Hamamelididae and derivatives. Tooth types believed to have a common ancestry are indicated by the letters within the same symbols, such as the circle or the diamond. Ch = Chloranthoid; P = Platanoid; U and \emptyset = Urticoid and Modified Urticoid; Sp = Spinose; and O = Other types. Possible affinity to the fossil "Platanoid" group and to *Sapindopsis* of Cretaceous age is indicated by question marks. Latex is indicated by the stippled pattern.

medial vein terminates at the tooth apex which is capped by a glandular nipple (i.e., papilla). 5. Numerous entire-margined forms such as *Disanthus*. 6. Primary veins approaching acrodromy (*Disanthus*). 7. Venation becoming pinnate by suppression of the basal primary veins (*Corylopsis*, *Hamamelis*, *Fothergillia*). The early Late Cretaceous form *Betulites* is a possible representative of this group as well.

Order 17. Eucommiales

Leaves simple; margin with glandular Platanoid Teeth; venation pinnate; secondary veins camptodromous; tertiary venation transverse; exstipulate; latex present.

Order 18. Urticales

Leaves simple; margin with non-glandular Urticoid Teeth; venation palmate; secondary veins craspedodromous; tertiary venation strongly transverse; stipulate, latex present.

Trends: 1. To palmately compound in Cannabaceae. 2. Venation trending from actinodromous to acrodromous in many Urticaceae and some Ulmaceae. 3. Venation becoming pinnate in many Ulmaceae and Moraceae. Ulmaceae also show a trend from pinnate leaves with symmetrical bases in *Chaetoptelea* to an asymmetrical base in *Ulmus*. 4. Characteristic composite intersecondary veins develop in the Moraceae by strengthening of the anastomoses of the alternate percurrent tertiary veins in the middle of the intercostal area.

Order 21. Fagales

Leaves simple; margin with non-glandular teeth having their midvein terminating at or somewhat beyond the apex (a modified Urticoid Tooth ? or possibly a Cunonioid Tooth in *Trigonobalanus* ?) or with Spinose Teeth; venation pinnate; tertiary venation strongly transverse; stipulate. Leaf affinities uncertain.

Order 22. Betulales

Leaves simple; margin with non-glandular, possibly modified Urticoid Teeth; venation pinnate although the basal pair of secondaries is possibly homologous to the lateral primaries; secondary veins craspedodromous; tertiary venation strongly transverse; stipulate.

Order 23. Balanopales

Leaves simple; margin entire; venation pinnate; secondary veins irregular camptodromous; tertiary venation random; exstipulate.

Order 24. Myricales

Leaves simple; margin toothed; venation pinnate; secondary veins semi-craspedodromous; laminar glands present; stipulate. The leaves of this and the preceding order provide no systematically important characters; thus Takhtajan's assignment is retained.

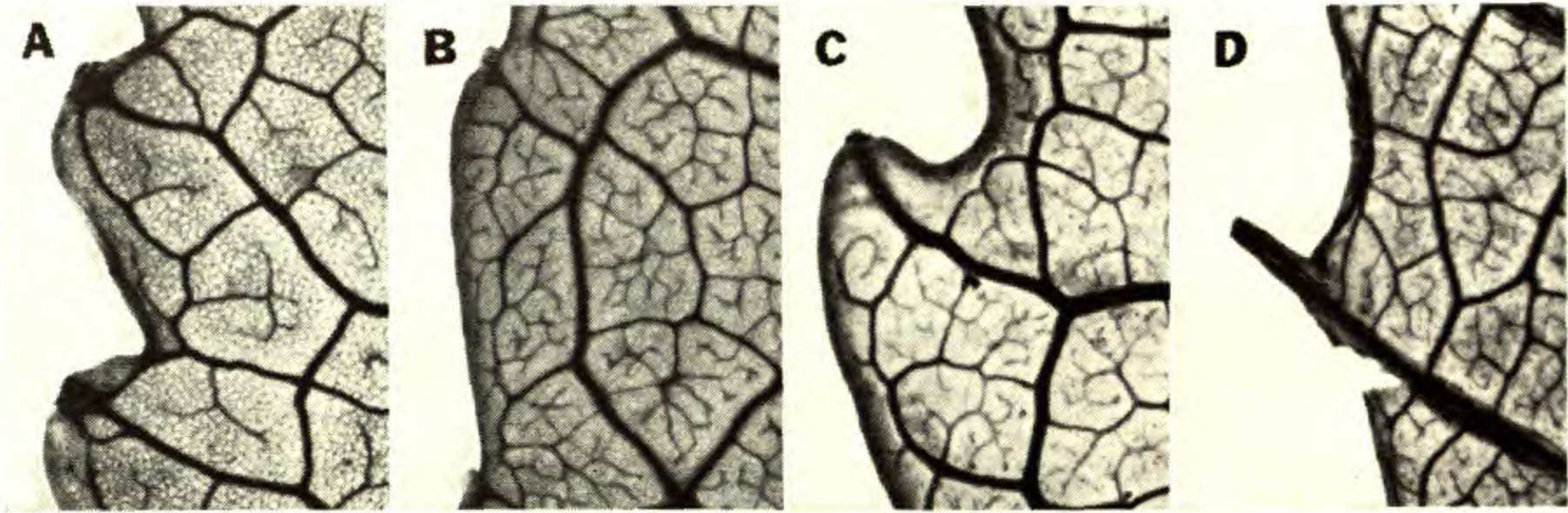


FIGURE 11. Tooth types of the Hamamelididae; all $\times 10$.—A. Chloranthoid; *Tetracentron sinense* Oliv. (Tetracentraceae); China: Hupeh, Wilson 2156 (US).—B. *Cercidiphyllum japonicum* Sieb. & Zucc. (Cercidiphyllaceae); Japan: Nikko, Collector Unknown (US 1314866).—C. *Altingia excelsa* Noronka (Hamamelidaceae); China: Yunnan, Rock 7174 (US).—D. *Corylopsis glabrescens* Franch. & Sav. (Hamamelidaceae); USA: Pennsylvania, Walker 7663 (US).

Order 25. Juglandales

To the subclass Rosidae; cf. Wolfe (1973).

Order 26. Leitneriales

Leaves simple; margin entire; venation pinnate; secondary veins camptodromous; tertiary venation strongly transverse.

Hamamelid Tooth Types

1. *Chloranthoid*—Ch (Figs. 2, 11)—Trochodendrales and possibly in a modified form in the Cercidiphyllales. Described under the Magnoliidae.

2. *Platanoid*—P (Figs. 2, 11)—Eupteleales, some Hamamelidales (*Platanus*, some Hamamelidaceae), Eucommiales. Teeth with a medial secondary vein becoming attenuated toward a glandular apex where it opens into a cavity or foramen; medial vein accompanied by higher order laterals forming a series of brochidodromous loops with the upper pair converging on, but not reaching, the medial vein.

3. *Urticoid*—U (Figs. 2, 11)—Urticales. A non-glandular tooth having a medial secondary vein terminating at or near its apex with convergent higher order lateral veins. A somewhat modified form (\cup) which is shorter and broader than the typical Urticoid Type is found in the Fagales and the Betulales.

4. Various other types—either highly specialized or derived:

a. *Spinose*—Sp (Fig. 2)—Hamamelidaceae (*Sinowilsonia*, *Corylopsis*), and some Fagales. Medial vein projecting beyond the tooth apex; non-glandular, possibly derived from the Platanoid or Urticoid types by recession of the margin.

b. *Fothergillia Type*—*Fothergillia*. Medial secondary terminating at the base of a clear glandular apical nipple or papilla; convergent higher order lateral veins present; tooth possibly derived from the Platanoid Type.

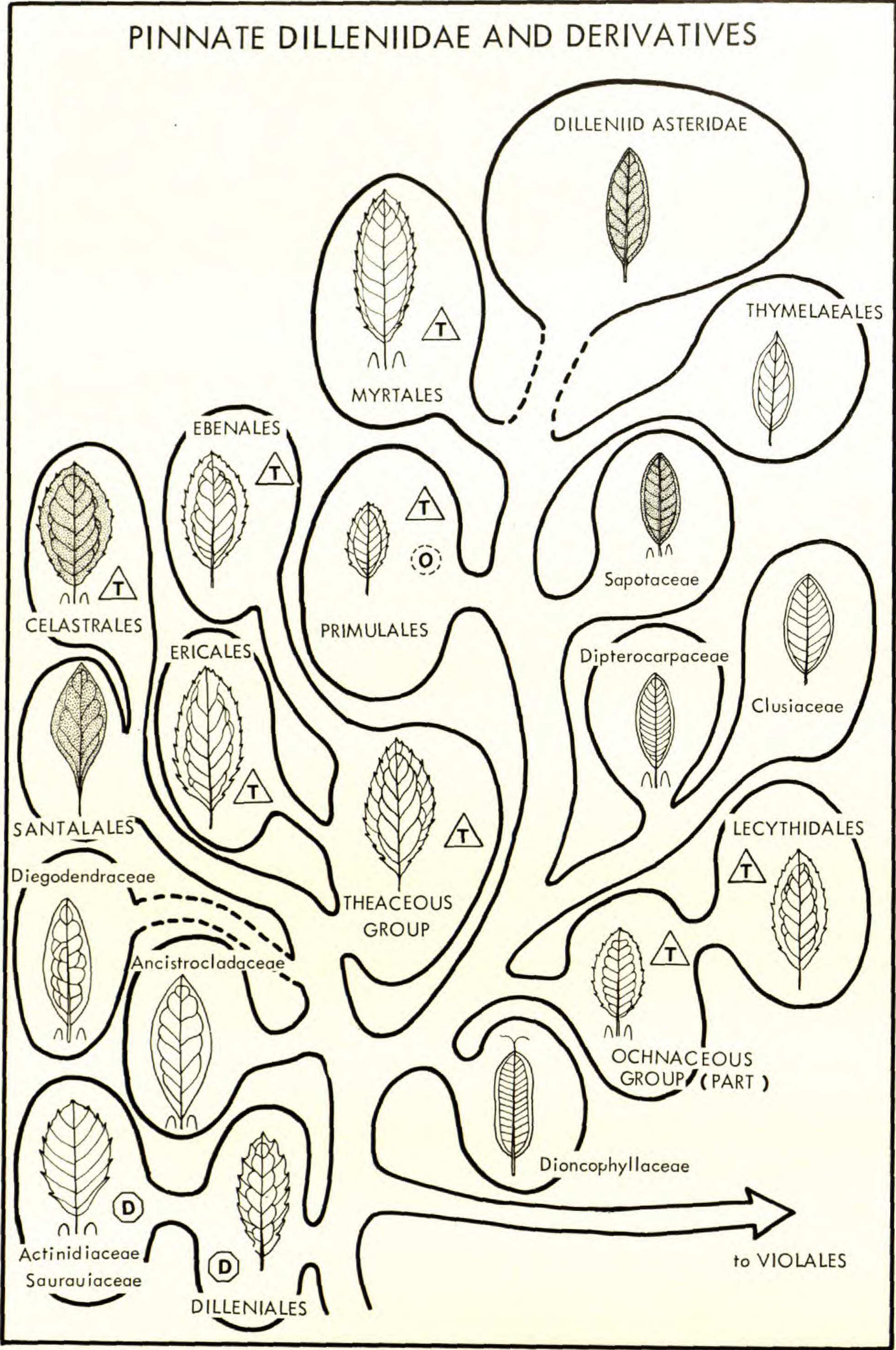


FIGURE 12. Leaf affinities in the Pinnate Dilleniidae and derivatives. Separation into a Theaceous Group on the left and an Ochnaceous Group on the right is shown in the diagram.

SUBCLASS D. CARYOPHYLLIDAE

Leaves simple; margin entire; venation pinnate; secondary veins irregularly brochidodromous; tertiary venation poorly developed, random and not transverse; leaves thick and fleshy or mealy, staining poorly in Safranin O; stipulate (Fig. 7).

Trends: 1. Strengthening of the basal pair of secondaries into primaries with the development of incipient basal lobes, giving rise to a tri-nerved, halberd-shaped leaf. 2. Many xerophytic and halophytic reductions especially toward oblong, entire-margined leaves with tri-nerved, imperfect acrodromous venation. 3. In secondarily woody, arborescent forms such as *Coccoloba* and *Charpentiera* the intercostal venation becomes transversely oriented. 4. Fusion of separate stipules into the basal sheath.

The orders of the Caryophyllidae are not analyzed in this survey.

SUBCLASS E. DILLENIIDAE

Leaves basically simple; margin toothed; venation pinnate; secondary veins semicraspedodromous; tertiary venation random with a tendency toward admedial orientation; glands present on teeth; stipulate (Figs. 12–13).

Trends: 1. Development of pinnately compound leaves in the Crossosomataceae and Quiinaceae. 2. Glandular teeth modified in a number of ways, especially in the Palmate Dilleniids, or lost. 3. Development of the Theoid Tooth in the ancestor of the Theaceous and Ochnaceous Alliances of the Pinnate Dilleniids and of the Palmate Dilleniids and further modifications of this type. 4. Development of actinodromous venation (leading to campylodromous) in the Palmate Dilleniids. 5. Development of a strongly transverse tertiary venation in the Dilleniales, the Actinidiaceous Group, and in the Palmate Dilleniids. 6. Development of tertiary venation paralleling the secondary veins in the Ochnaceous Alliance of the Pinnate Dilleniids. 7. Development of an intramarginal vein in the Ochnaceous Alliance and in the Primulales and the Myrtales. 8. Loss of stipules in many of the higher Dilleniidae as well as in scattered families. 9. Becoming laticiferous in numerous lines.

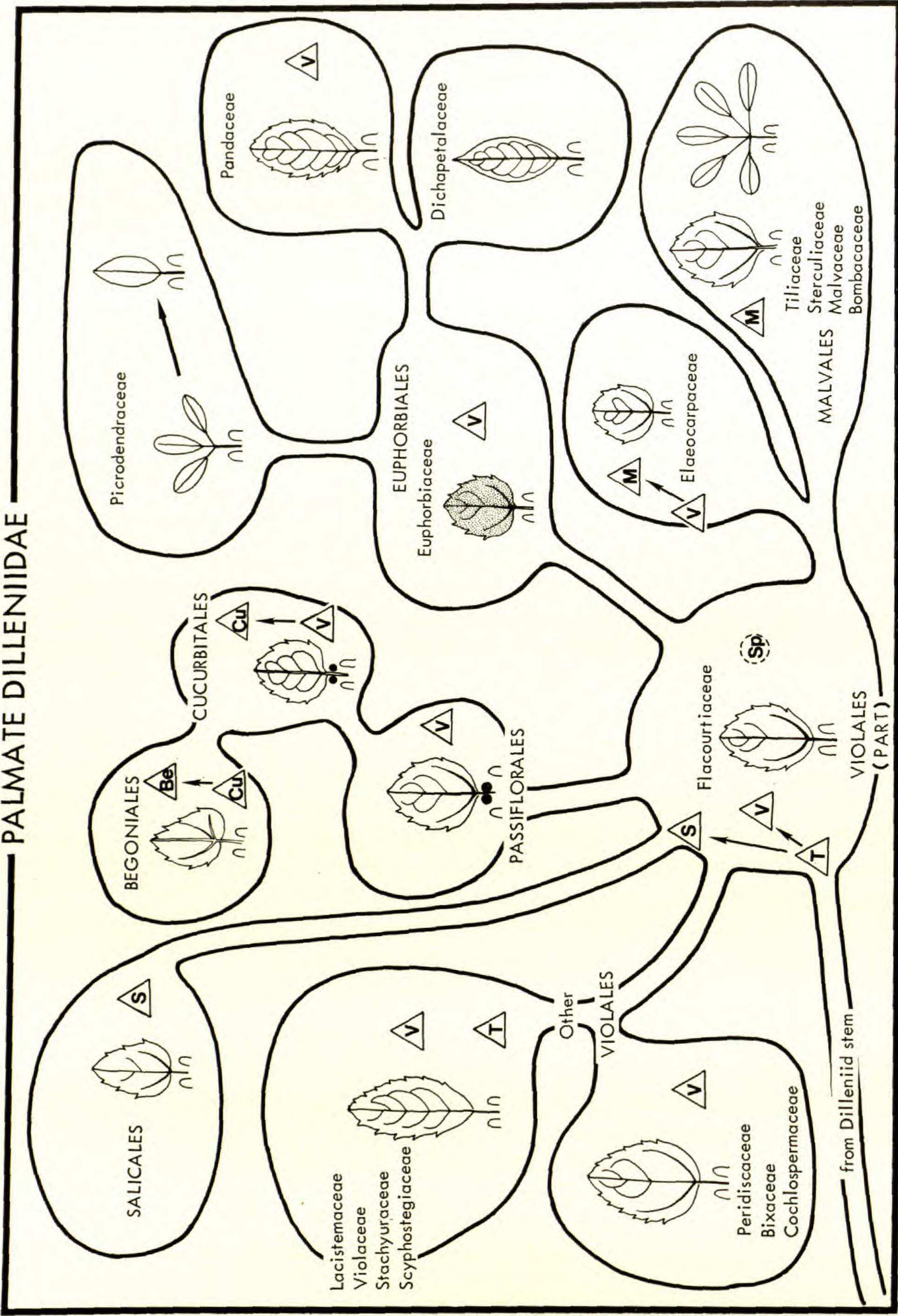
I. PINNATE DILLENIIDAE

Leaves basically simple; margin with glandular teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation random with a tendency toward admedial orientation; stipulate (Fig. 12).

Trends: 1. Development of the glandular setaceous Theoid Tooth in the forerunner of all but the Dilleniales and their inferred derivatives the Actinidiaceous Group (Figs. 3, 15). 2. Development of the Dillenioid Tooth with a clear glandular or expanded apex in the Dilleniales, or its retention there as a primitive

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Note also the inferred derivation of the Dilleniid-Leafed Asteridae from the Ochnaceous Group. Dillenioid Tooth type is indicated by the letter D in the hexagon, the Theoid Tooth by the T in the triangle, and other types by the letter O within the dashed circle. Latex is indicated by the stippled pattern.



feature, and its modification into a Spinose Tooth (Fig. 15). 3. Often with highly characteristic apical prolongation of the secondary loops in the Theaceous Alliance (Fig. 14). 4. Development of an intramarginal vein in the Ochnaceous Alliance. 5. Development of strongly percurrent tertiary venation in the Dilleniaceae, Actinidiaceae, and Saurauiceae. 6. Development of weakly transverse intercostal venation in the Theaceous Group and of intercostal venation paralleling the secondaries in the Ochnaceous Group.

Order 31. Dilleniales

Leaves simple; margin with Dillenioid Teeth having a clear glandular or expanded apex; venation pinnate; secondary veins probably basically semi-craspedodromous; intercostal venation random; stipulate.

Trends: 1. Development of an intramarginal vein (*Hibbertia*) (Fig. 6). 2. Development of craspedodromous secondary venation. 3. Development of rigidly percurrent tertiary venation in all genera of the Dilleniaceae except *Hibbertia*.

Leaves of this order, as presently constituted, do not include enough generalized characters to be regarded as ancestral to those of the remaining Dilleniids. Only *Hibbertia* has a generalized venation pattern, but most of the toothed forms of this genus have a clear glandular vein termination. However, teeth of the Australian species *Hibbertia dentata*, which have clear glandular deciduous tips, possibly represent the survival of a tooth type which later became the opaque glandular setaceous Theoid type which appears to be basic for all of the remaining Dilleniids except the Actinidiaceous Group.

31a. Actinidiaceous Group (including the Saurauiceae)

Apparently derived directly from the Dilleniales. Leaves simple, margin with Dillenioid Teeth; venation pinnate; secondary veins craspedodromous; tertiary venation rigidly percurrent; stipulate.

A. Theaceous Alliance

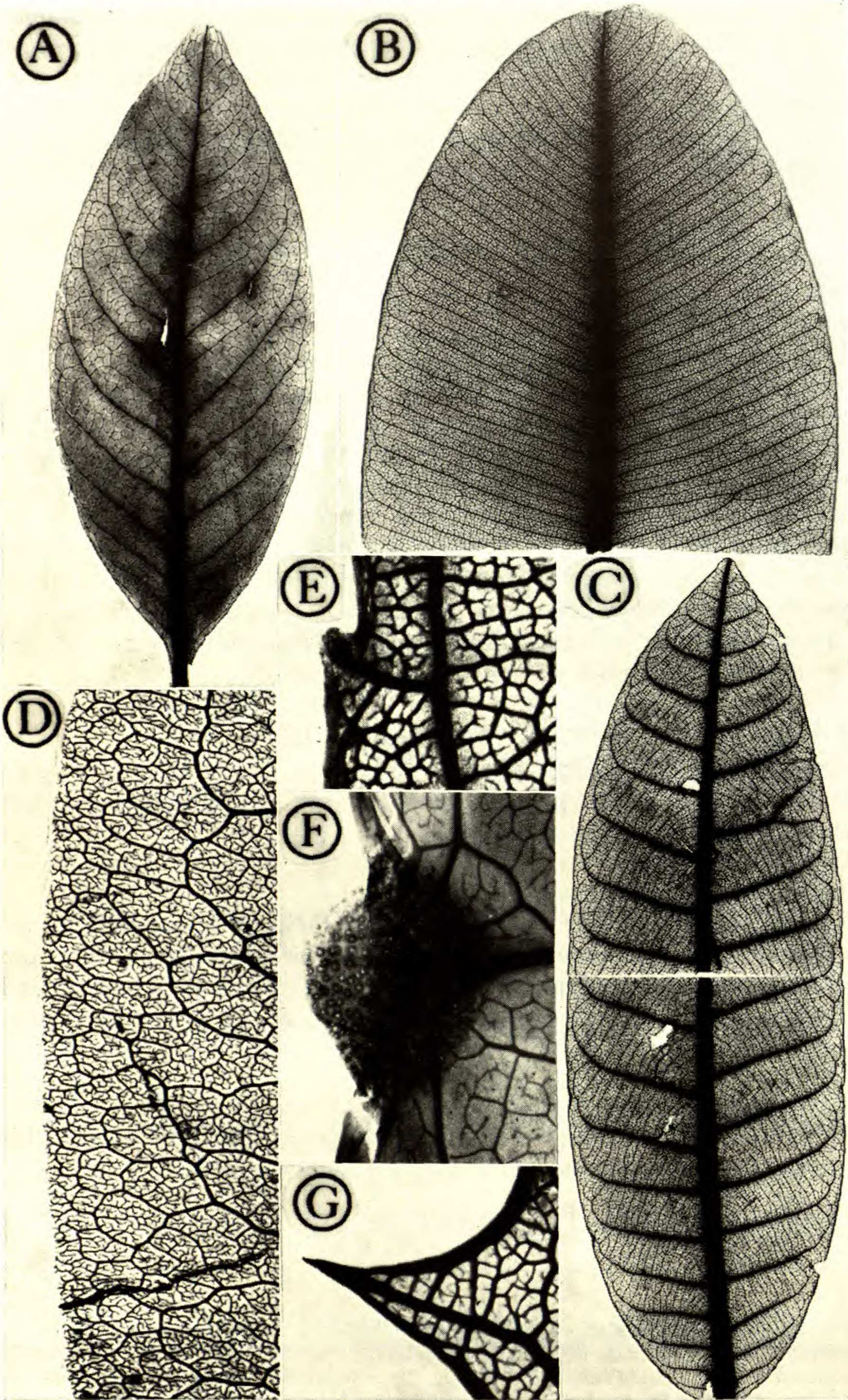
A morphological grouping of those Pinnate Dilleniid leaves having margins with Theoid Teeth; secondary veins basically brochidodromous often forming highly ascending arches (Fig. 14); tertiary venation tending to become at least weakly transverse rather than parallel to the secondaries as in the Ochnaceous Alliance; exstipulate.

33. Theaceous Group (Takhtajan's Order 33, Theales, in part, consisting of Theaceae, Marcgraviaceae, Pentaphylacaceae, Tetrameristaceae, Caryocaraceae, Asteropeiaceae, Pellicieraceae, Bonnetiaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins

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FIGURE 13. Leaf affinities of the Palmate Dilleniidae. Derivatives of the Theoid Tooth are indicated by the letter in the triangular symbol. T = Theoid Tooth, V = Violoid Tooth, S = Salicoid Tooth, Cu = Cucurbitoid Tooth, Be = Begonioid Tooth, M = Malvoid Tooth, Sp = Spinose Tooth. Presence of latex is indicated by the stippled pattern. Acropetiole glands indicated by the dark circles on the petioles of the Passiflorales and Cucurbitales.



brochidodromous often with ascending arches; tertiary venation random to weakly percurrent; basically exstipulate.

Trends: 1. Loss of marginal teeth followed by loss of marginal glands due to marginal enrollment during ontogeny. 2. Increase in transverse tertiary vein orientation. 3. Rarely becoming laticiferous as in *Ficalhoa* (Theaceae).

Order 41. **Ericales** (excluding the Saurauiaceae and the Actinidiaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate, secondary veins ascending brochidodromous; tertiary venation only weakly transverse; exstipulate.

Trends: 1. Loss of marginal teeth through marginal enrollment during ontogeny. 2. Increasing randomization of the intercostal venation.

In both the Ericales and the Ebenales the weakly transverse intercostal venation tends to be compensated for by the distal branching of the secondaries into a reticulodromous pattern. These secondary branches are then joined to brace the leaf margin (Fig. 14).

Order 42. **Diapensiales**

Not analyzed.

Order 43. **Ebenales** (excluding the Sapotaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins eucamptodromous to ascending brochidodromous to reticulodromous with the margin frequently braced by the anastomosing distal branches of the secondaries; tertiary venation ramified to irregularly transverse; exstipulate; latex absent.

Trends: 1. Loss of marginal teeth. 2. Tertiaries becoming moderately percurrent (*Diospyros*).

Order 61. **Celastrales**

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins brochidodromous with apically elongated arches; tertiary veins weakly transverse; stipulate; latex present.

Trends: 1. To entire margins. 2. Eucamptodromous secondary venation. 3. Craspedodromous secondaries in some Aquifoliaceae. 4. Veinlets with numerous branches in Icacinaceae.

In the Takhtajan and Cronquist systems this order is allied to the Rosidae although it shows no trace of a compound-leafed ancestry (Cronquist, 1968:

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FIGURE 14. Some features of leaves of Dilleniidae.—A. Apical prolongation of brochidodromous arches; *Schima confertifolia* Merr. (Theaceae); China: Kwangtung, Levine 1346 (US); $\times 1$.—B–C. Patterns of ochnalean venation.—B. *Kielmeyera coriacea* Mart. (Clusiaceae); Brazil: Irwin *et al.* 10870 (US); $\times 1$.—C. *Caraipa punctatula* Ducke (Clusiaceae); Brazil: Ducke 35410 (US); $\times 1$.—D. Ericaceous reticulodromous marginal venation; *Befaria glauca* Humb. & Bonpl. (Ericaceae); Colombia: Cuatrecasas 13384 (US); $\times 5$.—E–G. Some inferred variants of the Theoid Tooth; all $\times 10$.—E. Violoid; *Banara domingensis* Benth. (Flacourtiaceae); Dominican Republic: Ekman 10898 (US).—F. Cucurbitoid; *Fevillea cordifolia* L. (Cucurbitaceae); Peru: Woytkowski 7607 (US).—G. Spinose; *Casearia crassinervis* Urb. (Flacourtiaceae); Cuba: Oriente Province, León & Allain 19331 (US).

255), a character we believe is basic to that subclass. In addition, two families of the Celastrales, the Aquifoliaceae and the Celastraceae, have Theoid Teeth with deciduous seta. In most of the Celastrales these teeth are strongly modified or the apex is turned inward close to the sinus, but typical Theoid Teeth occur in the two U.S. National Herbarium specimens identified as *Celastrus novoguineensis* Merr. and Perry (Eastern New Guinea: Mt. Wilhelm, E slope, 6 July 1959, 2770 m, Brass 30337; Arau, 21 October 1959, 1400 m, Brass 32222). In addition, leaves of the Celastrales show the same apically elongate secondary arches and generally weakly transverse tertiary venation as in the Theaceous Alliance of the Dilleniidae.

Placement of this order with centripetal stamen maturation in the Dilleniidae would indicate that this feature—rather than being a fundamental determinate of Rosid affinity, as in Cronquist's system—may have had an independent origin within the dilleniid line (see discussion in Philipson, 1974). Hutchinson (1973) also places the Celastrales within the context of the Dilleniidae when he derives it from either the Theales or the Tiliaceae.

Order 64. Santalales

Leaves simple, base tending to be decurrent into the petiole; margin entire (if the disputed Dipentodontaceae and Medusandraceae—both toothed—are excluded); venation basically pinnate; secondary veins irregularly brochidodromous in ascending arches, the basal pair decurrent into the top of the petiole; tertiary venation weakly and distantly transverse; veinlets highly branched; exstipulate; latex present. This basic leaf has many similarities with the exstipulate family Icacinaceae, to which Santalales are reported to be closely related by Takhtajan and Cronquist.

Trends: 1. Reduction of leaves to scales or their complete loss in some genera of the Loranthaceae, and in Cynomoriaceae and Balanophoraceae. 2. To decrease the angle of divergence of the basal secondaries, strengthen these veins (e.g., some Loranthaceae), and to develop acrodromous and actinodromous forms through the process of augmenting these basal secondaries (some Santalaceae, Loranthaceae, Cardiopteridaceae). 3. To eucamptodromy. 4. Reorientation of the tertiaries obliquely across the intercostal area either perpendicular or oblique to the midvein.

Order 5. Rafflesiales

Leaves, when present, reduced to scales, simple; margin entire; veins reduced to two orders, parallelodromous and dichotomously branched, with disjunct distal portions (Sreemadhaven & Hickey, in preparation); petiole lacking.

Leaf evidence for the assignment of this order is insufficient. We simply follow Cronquist here in relating it to the Santalales where superficially similar leaves occur in the more reduced parasitic forms.

B. Ochnaceous Alliance

A morphological grouping of those Pinnate Dilleniids with Theoid Teeth, secondary veins strongly brochidodromous, sometimes in ascending arches but

mostly tending to form an intramarginal vein; tertiary venation obliquely percurrent, tending to become oriented perpendicular to the midvein and eventually parallel to the secondaries (Fig. 12).

Trends: 1. Increased strengthening and straightening of the brochidodromous arch to form an intramarginal vein, accompanied by closer spacing of the secondaries, development of an intersecondary vein paralleling the secondaries, and reorientation of the tertiary system in the same direction (Fig. 14). 2. Loss of stipules. 3. Loss of marginal teeth. 4. Becoming laticiferous in certain lines.

33. Ochnaceous Group (Takhtajan's Order 33, Theales, in part, consisting of Ochnaceae, Lophiraceae, Dipterocarpaceae, Strasburgeriaceae, Ancistrocladaceae, Dioncophyllaceae, Diegodendraceae, Quinaceae, Medusagynaceae, Oncothecaceae, Clusiaceae, Hypericaceae, and Elatinaceae)

Leaves simple; margin with Theoid Teeth; venation pinnate; secondary veins strongly brochidodromous often forming an intramarginal vein by strengthening and straightening of the outer portion of the arc, more rarely ascending brochidodromous or eucamptodromous; secondaries tending to become closely spaced in the strongly brochidodromous forms; intercostal areas with a medial intersecondary vein to the arch; tertiary venation obliquely percurrent, tending to become oriented perpendicular to the midvein and eventually parallel to the secondaries; stipulate (Fig. 14).

Trends: 1. To pinnately compound leaves in the Quinaceae. 2. Formation of an intramarginal vein by strengthening and straightening of the brochidodromous secondary arches. Development of this vein as the principal barrier to tearing from the margin appears to be accompanied by withdrawal of the margin to a position just outside the intramarginal vein. Marginal teeth and glands are also progressively lost during this process and the tertiary intercostal veins often become oriented parallel to the secondaries. We infer that marginal withdrawal and loss of teeth is due to premature cessation of marginal growth and that the parallel orientation of the tertiary veins becomes possible where they are not needed as reinforcements against ripping from the margin. 3. Secondary redevelopment of apparently transverse tertiary veins by the strengthening and fusion of the quaternary vein segments connecting admedially orientated tertiaries with the concomitant reduction in strength of the tertiaries (Dipterocarpaceae).

Order 33b. Lecythidales (Lecythidaceae in the broad sense including the Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae)

Leaves basically simple; margin with Theoid Teeth; venation pinnate; secondary veins brochidodromous; tertiary venation admedially ramified to weakly transverse; exstipulate.

Family 155. Sapotaceae

Leaves simple; margin entire; venation pinnate; secondary veins irregularly brochidodromous to eucamptodromous; tertiary venation obliquely and irregularly percurrent, tending to be oriented perpendicular to the midvein; stipulate; latex present.

Trends: 1. Brochidodromous arch becoming straighter and more regular, forming an intramarginal vein in the Mimosopeae and in other genera such as *Butyrospermum* and *Planchonella*. 2. Secondaries becoming closely spaced in brochidodromous forms and a medial intersecondary vein developing (*Chrysophyllum*). 3. Tertiaries oriented parallel to the secondaries in the Mimosopeae.

This family with its latex system, trilacunar nodes, unitegmic ovules, pubescence of two-armed hairs, and ochnealean venation is anomalous within the Ebenales, which are without latex, unilacunar, often bitegmic, lacking in two-armed hairs, and have leaves of the thealean venation pattern.

Order 44. Primulales

Leaves simple; margin with Theoid Teeth (in Theophrastaceae only); secondary veins brochidodromous to eucamptodromous; tertiary venation irregularly transverse; exstipulate; latex absent.

Trends: 1. Loss of marginal teeth in most genera. Modified teeth are retained in *Maesa* (Myrsinaceae) where they are coarse, doubly concave, and have a glandular swelling at the end of a medial vein branch which frequently recurves upon entering the tooth. Primulaceae retain a swollen non-deciduous glandular cap. 2. Development of acrodromous leaves in *Jacquinia* possibly by strengthening of the double brochidodromous arches (an inner and an outer) characteristic of the Theophrastaceae. 3. Development of an intramarginal vein. 4. Orientation of tertiaries perpendicular to the midvein and in strongly brochidodromous forms these often become oriented parallel to the secondaries.

Order 47. Thymelaeales (including Didymelaceae)

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous and forming an intramarginal vein with the secondaries forking conspicuously as they join it; tertiary venation random to weakly transverse; glands lacking; exstipulate.

Trends: 1. Loss of intramarginal vein; secondaries become eucamptodromous. 2. Increasing irregularity of secondaries.

Order 54. Myrtales

Leaves simple; margin basically entire, but primitively with Theoid Teeth (Rhizophoraceae); venation pinnate; secondary veins brochidodromous; tertiary venation obliquely and irregularly percurrent; stipulate; latex absent.

Trends: 1. Development of intramarginal veins in most families, especially in the Myrtaceae. This is accompanied by reorientation of the transverse tertiary network parallel to the secondaries and development of a medial intersecondary vein. 2. Development of acrodromous venation apparently by strengthening of the outer intramarginal vein and the next highest secondary vein which forms an inner brochidodromous arch. Our model then postulates the broadening of these acrodromous secondaries into primaries and the migration of the upper pair to a basal position. Inferred transitions from brochidodromous with a weak intramarginal vein through suprabasal to basal acrodromous can be seen in the Memecylaceae into the Melastomataceae and independently in the Anisophyl-

- leaceae. 3. Development of eucamptodromous secondaries in the Combretaceae. 4. Loss of stipules.

Despite the absence of internal phloem in Rhizophoraceae, the leaf architecture of this family coincides closely with that of the Myrtalean families to which Takhtajan assigns it and not at all to the Cornales where Cronquist places it. We have thus treated its leaf architecture with the Myrtales.

Description of the leaf architecture of the Myrtales with the Dilleniidae presents another important case where leaf morphology yields evidence which runs counter to the assignment of an order to the Rosidae on the basis of other organs. In this case the ochnelean venation pattern, presence of Theoid Teeth, and the apparent lack of compound-leaf ancestors influence us to treat its leaf architecture with the Dilleniidae. On the other hand, the centripetal stamen maturation direction and the pollen of most of the Myrtales, except the Rhizophoraceae, indicate Rosid affinities (Doyle, personal communication). If the Rhizophoraceae is excluded from the order, then the Theoid Tooth is not part of Myrtalean leaf architecture, and the Myrtales possibly represent a trend in the Rosids paralleling the Ochnalean Group in developing strongly brochidodromous secondaries and intramarginal veins and in having modifications of the tertiary venation similar to the ochnelean pattern. More evidence, especially from carefully studied fossil leaves and comparative morphology, will be needed to resolve this seeming contradiction.

II. PALMATE DILLENIIDAE

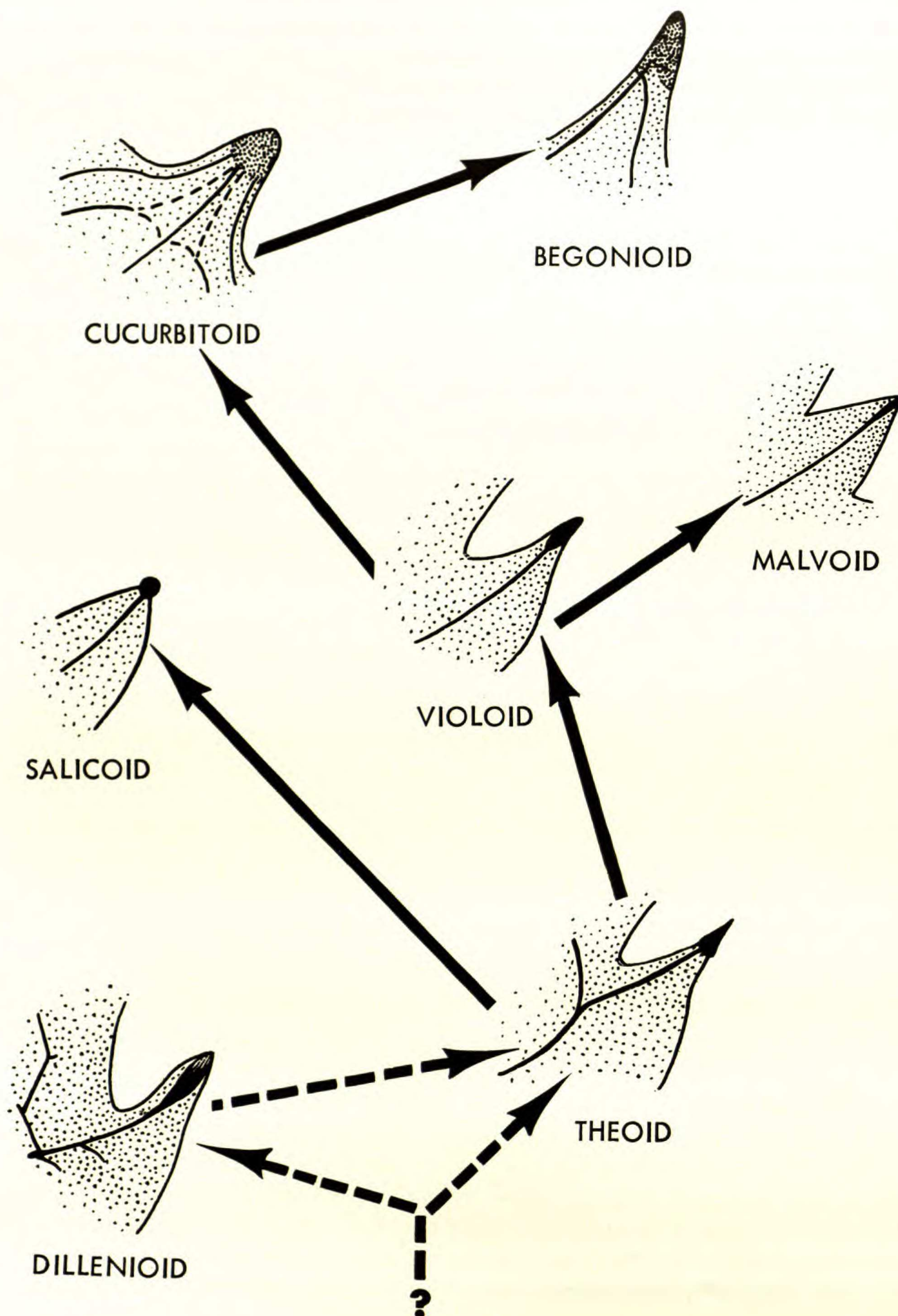
Leaves basically simple; margin with glandular teeth; venation actinodromous; secondary veins semicraspedodromous; tertiary venation weakly transverse; stipulate (Fig. 13).

Trends: 1. Leaves becoming palmately compound in some Passiflorales, Malvales, and Euphorbiales. 2. Modification of the primitive Theoid Tooth by fusion of the glandular seta to the tooth apex in the Violales, Passiflorales, Malvales, and Euphorbiales; by loss of glandular function in the Malvales; or by other specialized modifications in the Violales, Salicales, Cucurbitales, and Begoniales (Fig. 15). 3. Development of pinnate venation by weakening of the lateral primaries in all orders but Begoniales. 4. Development of strongly transverse tertiary venation which is characteristically oriented in a concentric fashion in relation to the leaf base. 5. Becoming laticiferous in the Euphorbiales.

Order 34. Violales

Leaves simple; margin with Theoid Teeth; venation imperfectly or incipiently actinodromous; secondary veins semicraspedodromous; tertiary venation weakly transverse; stipulate.

Trends: 1. Development of strongly actinodromous or campylodromous leaves in the Peridiscaceae, Bixaceae, Cochlospermaceae, some Violaceae, and many Flacourtiaceae. The primitive tribe Rinoridae of Violaceae has pinnate leaves with the basal secondaries originating from the top of the petiole at a somewhat lower angle than those above, indicating either common origin from the same incipiently actinodromous trend as the Flacourtiaceae (*Berberidopsis*)

DILLENIID TOOTH TYPES AND THEIR PROPOSED
PHYLOGENY

or suppression of the lateral primaries. 2. Development of pinnate venation in a number of families by suppression of the lateral primaries. 3. Modification of the Theoid Tooth (Fig. 2) found in many genera of the basal family Flacourtiaceae (including the most primitive *Berberidopsis* and *Carpotroche*) within the family to the: a. Violoid Tooth in flacourtiaceous genera, such as *Xylosma* and *Homalium*, and in the Violaceae, Stachyuraceae, and Cochlospermaceae. b. Salicoid Tooth in the Idesidae of the Flacourtiaceae and thus to the Salicales (Fig. 16). 4. The Theoid Tooth is retained in the Lacistemataceae.

Order 35. Passiflorales

Leaves basically simple; margin with Violoid Teeth; venation actinodromous; acropetiolar nectaries present; stipulate.

Trends: 1. Leaves becoming palmately compound by dissection of lobes. 2. To pinnately veined, simple leaves with basally congested secondary venation. 3. Loss of stipules and nectaries.

Order 36. Cucurbitales

Leaves simple; margin with Violoid Teeth; venation actinodromous; acropetiolar nectaries present; stipulate.

Trends: 1. Development of the Cucurbitoid Tooth from the Violoid Tooth. 2. Development of campylodromous venation. 3. Loss of acropetiolar nectaries.

Order 37. Begoniales

Leaves simple; margin with Cucurbitoid Teeth; venation actinodromous; stipulate; leaf with a pervasive asymmetry of form and venation.

Trends: 1. Development of the Begonioid Tooth in the Begoniaceae. 2. Loss of stipules in the Datisceae.

Order 40. Salicales

Leaves simple; margin with Salicoid Teeth inferred to be of common origin with those of *Idesia* in the Flacourtiaceae; venation actinodromous; basilaminar glands present; stipulate.

Trends: 1. Loss of teeth in Arctic species of *Salix*. 2. Venation becoming pinnate in *Salix*.

Order 45. Malvales

Leaves simple; margin with the non-glandular Malvoid Tooth, although primitively with the Violoid Tooth (as in Elaeocarpaceae); venation actinodromous; tertiary venation percurrent, frequently concentrically so; stipulate.

Trends: 1. Palmate dissection of the leaf in Elaeocarpaceae, Tiliaceae, Sterculiaceae, and Bombacaceae. 2. Violoid Tooth becoming the non-glandular Malvoid type in genera of the Elaeocarpaceae, Sterculiaceae, Tiliaceae, and Bombacaceae. 3. Development of both perfect actinodromous and of pinnately veined forms by

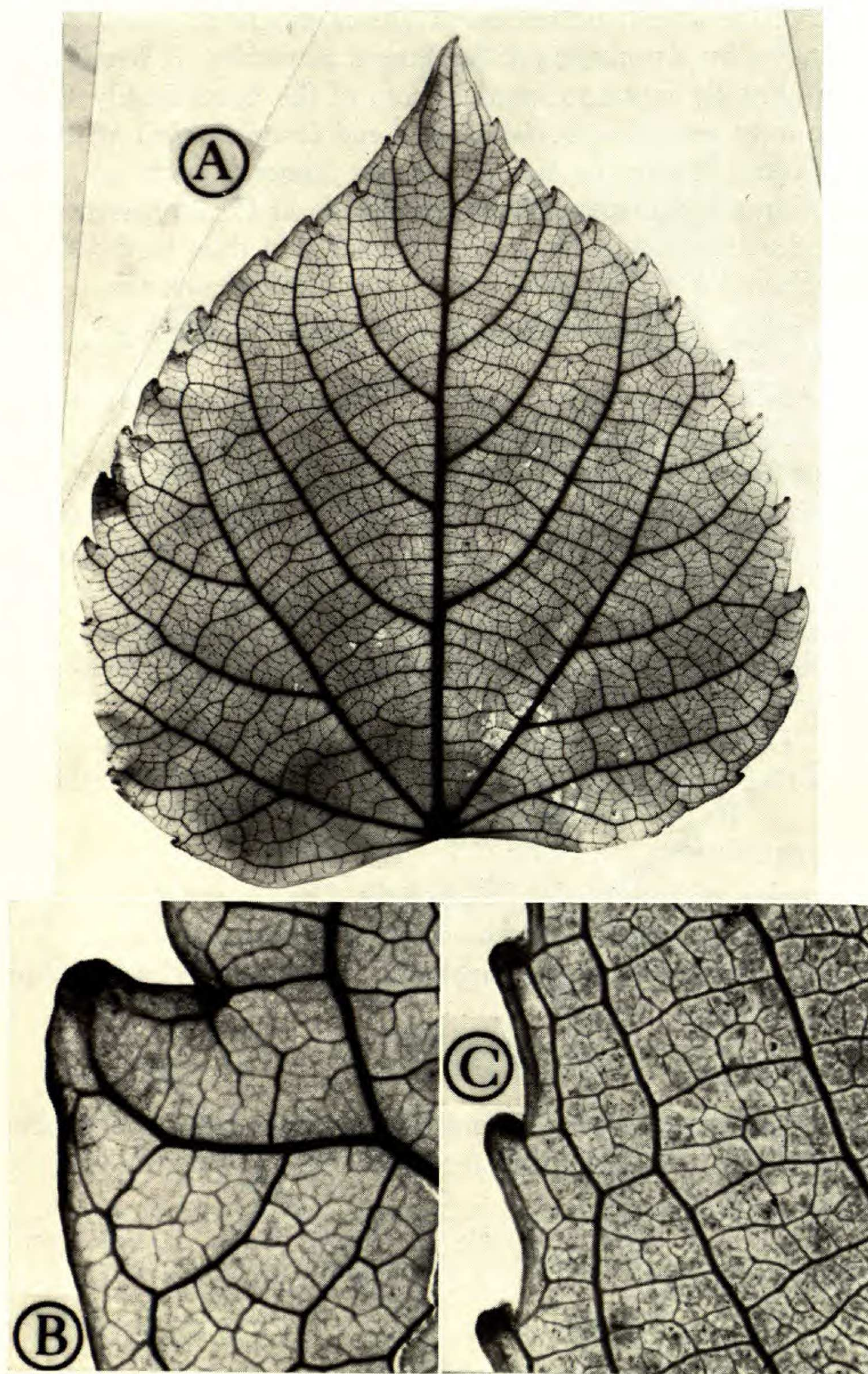
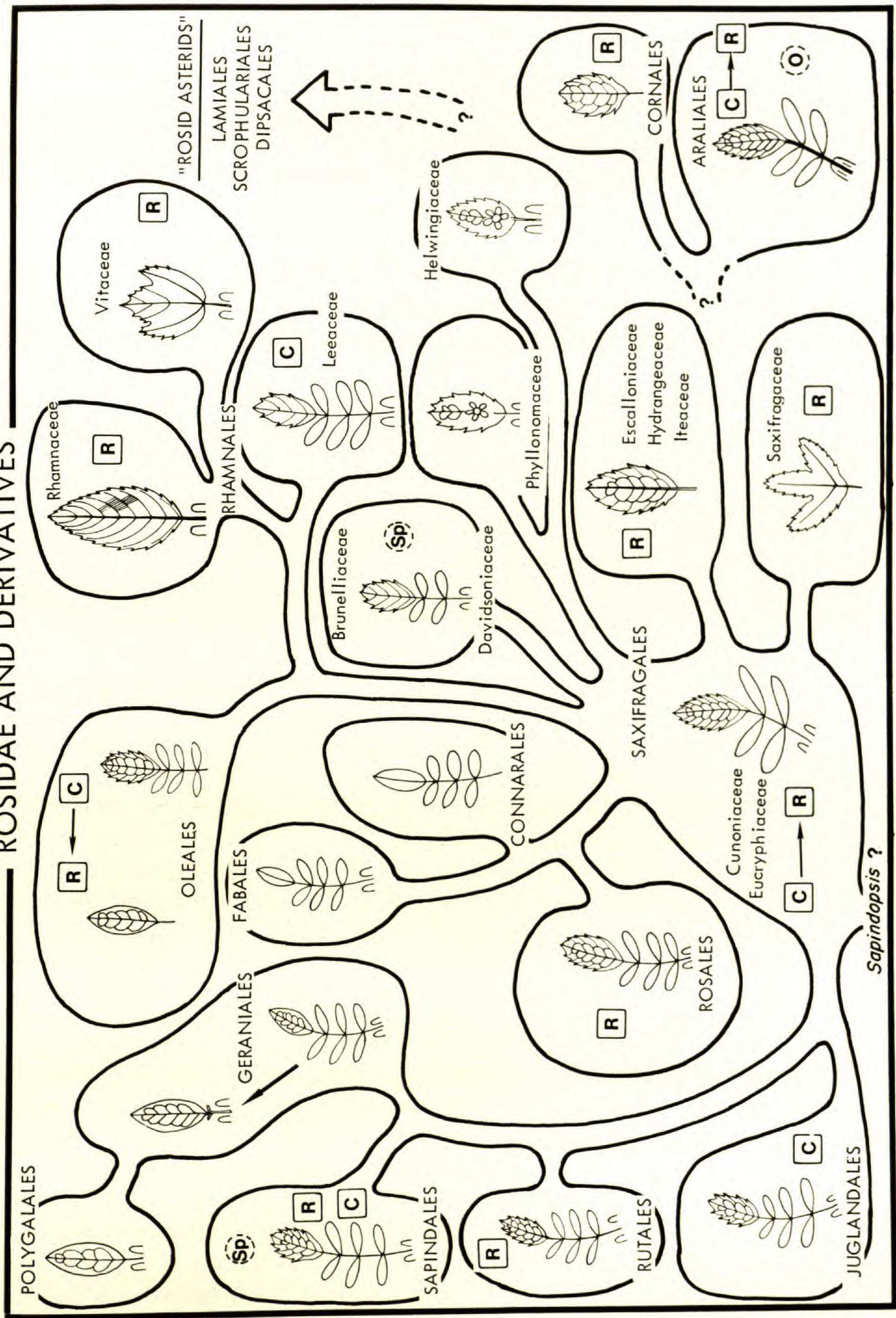


FIGURE 16. Salicoid teeth found in *Idesia polycarpa* Maxim. (Flacourtiaceae); Japan: Nanokawa, *Collector Unknown* (US).—A—B. *Idesia* with the tooth enlarged $\times 1$ and $\times 10$, respectively.—C. Salicoid Tooth in *Salix fragilis* L. (Salicaceae) for comparison; USA: Iowa, *Thorne 13312* (US); $\times 10$.

→
FIGURE 17. Leaf affinities of the Rosidae and derivatives. Possible affinity to the Lower Cretaceous genus *Sapindopsis* is indicated by the question marks. Origin of the Cornales and Araliales is uncertain, as is that of the Rosid Asterids. The symbol on the leaves of Phyllonomaceae and Helwingiaceae represent attached inflorescences. The Cunonioid Tooth and its derivative the Rosoid Tooth are indicated by the letters C and R, respectively, within the squares. Sp within the dashed circle indicates the Spinose Tooth and O in the same symbol indicates a specialized type of tooth of unknown derivation.

ROSIDAE AND DERIVATIVES



reinforcement or suppression of the lateral primary veins in a possible imperfect actinodromous ancestral form.

Order 46. Euphorbiales

Leaves basically simple; margin with glandular Violoid Teeth; venation imperfect actinodromous; tertiary venation transverse; stipulate; latex present.

Trends: 1. Palmate dissection of the leaf in some Picrodendraceae, Euphorbiaceae, Pandaceae, Dichapetalaceae. 2. Leaf becoming perfect actinodromous. 3. Development of prominent basilaminar and acropetiole glands.

Principal Dillenioid Tooth Types

1. *Dillenioid*—D (Fig. 15)—Dilleniaceae, Actinidiaceae. Medial vein of the tooth terminating in a clear glandular expanded (papillate) apex, vein often projecting beyond the tooth apex.

2. *Theoid*—T (Figs. 2, 15)—Theaceae, Ochnaceae. Medial vein of the tooth running to the apex, vein end expanded and congested with opaque material. Tooth apex capped by an opaque deciduous seta.

3. *Violoid*—V (Figs. 14–15)—Violaceae, Cochlospermaceae. Medial vein of the tooth running to the apex where it expands into an opaque glandular termination, deciduous apical seta absent.

4. *Salicoid*—S (Figs. 2, 15, 16)—*Idesia*, Salicaceae. An inferred modification of the Theoid Tooth where the seta is retained as a dark, but not opaque, non-deciduous spherical callosity fused to the tooth apex.

5. *Malvoid*—M (Fig. 15)—Malvaceae, Bombacaceae. Medial vein of the tooth running to the apex, non-glandular or apparently so.

✓ 6. *Cucurbitoid*—Cu (Figs. 14–15)—Cucurbitaceae, Datisceae. Medial vein of the tooth ending in a translucent apical pad of densely packed cells (tylate apex). Lateral veins present and either fusing with the medial vein or connivent with it and terminating in the tylate apex.

✓ 7. *Begonioid*—Be (Fig. 15)—Begoniaceae. An inferred asymmetrical modification of the Cucurbitoid Type in which one of the lateral veins appears to be strengthened at the expense of the medial and second lateral.

8. *Spinose*—Sp (Fig. 14)—Flacourtiaceae.

SUBCLASS F. ROSIDAE

Leaves basically pinnately compound; margin with glandular Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; stipulate; latex absent (Fig. 17).

Trends: 1. Development of palmately lobed or palmately compound leaves by inferred shortening of the pinnate rachis in the Saxifragales, Hippuridales, Sapindales, Geraniales, Cornales, and Rhamnales. 2. Development of simple leaves in most orders through reduction to one of the leaflets of pinnate leaves. 3. Origin of the Rosoid Tooth from the Cunonioid Tooth in several lines, apparently independently, as the result of broadening of the tooth (Fig. 18). 4. Origin of the Spinose Tooth from the Cunonioid Tooth in the Sapindales and

ROSID TOOTH TYPES AND THEIR PROPOSED PHYLOGENY

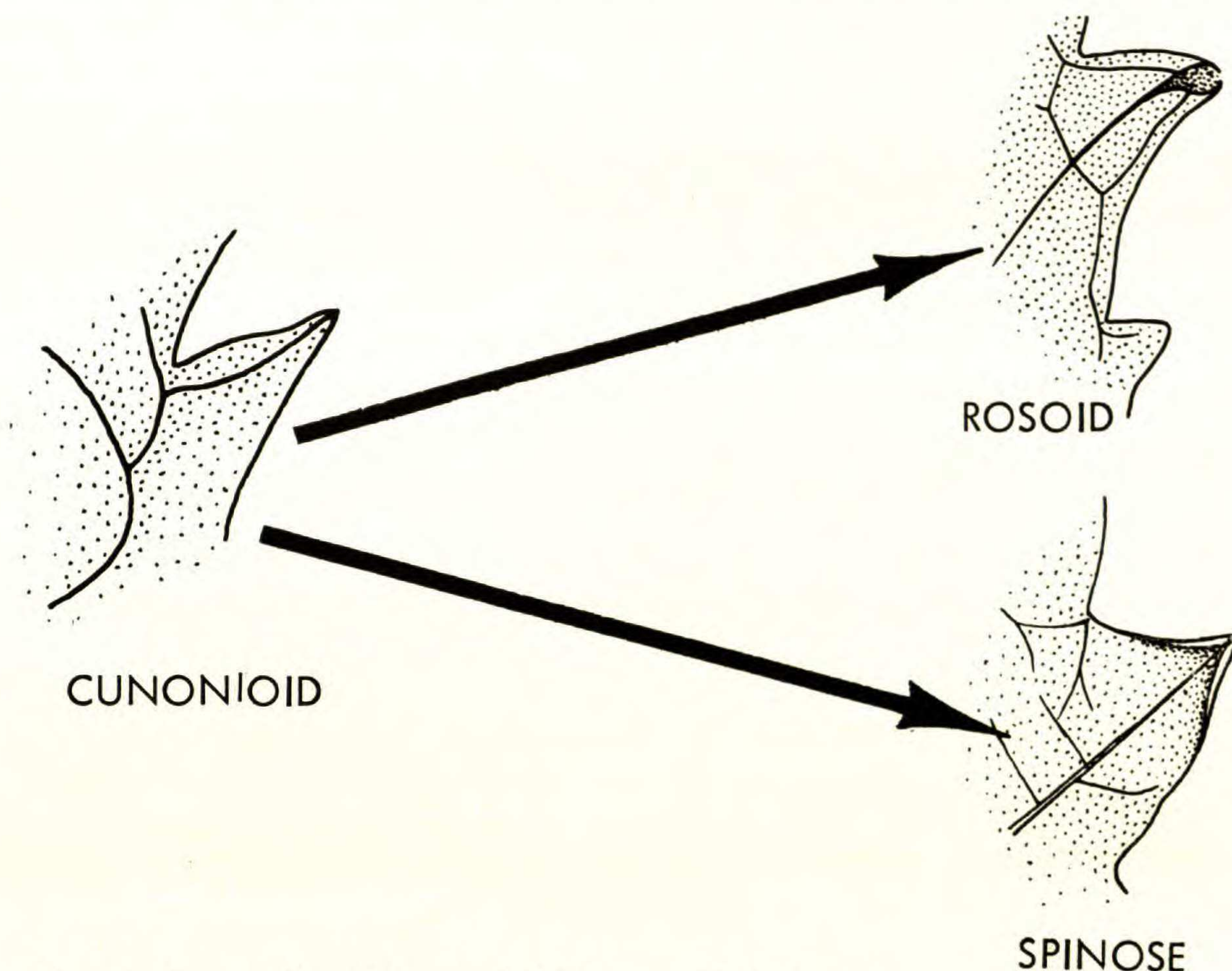


FIGURE 18. Rosid tooth types and their proposed phylogeny.

Saxifragales (Fig. 18). 5. Camptodromous and craspedodromous secondary vein configurations developing from the semicraspedodromous condition. 6. Origin of laminar glands in the superorder Rutanae.

A complex of pinnately compound leaves known as *Sapindopsis* from the Albian (upper Lower Cretaceous) of the Potomac Group of the eastern United States and of correlative strata elsewhere in the Northern Hemisphere displays a number of characters of form, venation, and margin which are consistent with primitive rosids. The earliest of these (*S. magnifolia* Fontaine) is pinnatifid with irregularly brochidodromous venation. Later forms, however, are truly pinnate and include members with teeth having secondary veins which branch near the sinus below the teeth, sending one branch to the tooth apex along the apical side of the tooth and the other into the area of the sinus or to the super-adjacent secondary. Although the shape and venation of these teeth is similar to that of the Cunonioid Tooth, a distinct spine or process at the tooth apex is unlike anything now found in the Rosidae. Some of these later *Sapindopsis* leaves also have laminar resin dots (Doyle & Hickey, in press).

Order 48. Saxifragales

Leaves basically pinnately compound; margin with Cunonioid Teeth; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands

absent; stipulate. (Excluding Paracryphiaceae which has modified but non-rosid teeth.)

Trends: 1. Leaves becoming palmately compound and palmately lobed in the Saxifragaceae and Grossulariaceae through inferred shortening of the pinnate rachis. 2. Leaves becoming simple in the Escalloniaceae, Hydrangeaceae, Iteaceae, and Pterostemonaceae. 3. Development of the Rosoid Tooth in the Saxifragaceae, Grossulariaceae, Escalloniaceae, Hydrangeaceae, and possibly others. 4. Development of a Spinose Tooth and pure craspedodromous venation in the Davidsoniaceae and Brunelliaceae. 5. Development of entire margins in Pittosporaceae and Bruniaceae. 6. Stipules lost in the Hydrangeaceae, Montiniaceae, Roridulaceae, Pittosporaceae, Byblidaceae, and Bruniaceae.

Order 49. Rosales

Leaves basically pinnately compound; margin with Rosoid Teeth having a clear glandular (hydathodal?) apical foramen; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; laminar glands absent; stipulate.

Trends: To simple, entire leaves in the Chrysobalanaceae and to simple leaves with acropetiole nectaries in the subfamily Prunoideae.

Order 50. Fabales

Leaves basically pinnately compound; margin entire; venation pinnate; secondary veins brochidodromous; stipules present.

Trends: Many and various with loss of leaflets, fusion of leaflets, and loss of the entire blade, among others.

Order 51. Connarales

Leaves pinnately compound; margin entire; exstipulate.

Order 55. Hippuridales

Leaves basically simple; margin with Rosoid Teeth; exstipulate.

Trends: 1. Leaves elliptic to linear with pinnate craspedodromous venation and Rosoid Teeth, or leaves reduced or filiform in the Haloragaceae. 2. Leaves simple, palmately lobed, with Rosoid Teeth and actinodromous venation in the Gunneraceae. 3. Leaves scale-like in the Hippuridaceae.

Order 25. Juglandales

Leaves pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands resin secreting, sessile, stalked, capitate, and peltate; stipulate.

The presence of pinnately compound leaves having well developed Cunonioid Teeth make them anomalous in the Hamamelididae where they were placed by Takhtajan and Cronquist. Resinous secretions and peltate laminar glands similar to those in the Myricaceae and the Fagaceae occur abundantly in the rosid order Rutales. Although the wood anatomy of the Juglandales is more primitive than that of the Rutales, and workers such as Heimsch & Wetmore (1939) and Withner

(1941) have denied any strong relationship between the Juglandales and Rutales on this basis, similarities do exist (Handel-Mazzetti, 1932; Copeland & Doyel, 1940) which allow at least collateral derivation of the two lines. Such a scheme also requires that the tricolporate to triporate pollen and reduced inflorescences of Juglandales be convergent with the Betulaceae, Myricaceae, and Casuarinaceae, probably as independent adaptations to wind pollination rather than the result of common ancestry.

Trend: Loss of stipules in Juglandaceae.

Order 56. Rutales

Leaves basically pinnately compound; margin with Rosoid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; laminar glands, resin secreting, sessile, stalked, capitate, and peltate; stipulate.

Trends: 1. Loss of marginal teeth resulting in a lamina whose secondaries are either eucamptodromous (Anacardiaceae) or rigidly brochidodromous (Burseraceae) and which turn upward abruptly near the margin. 2. Loss of laminar glands. 3. Loss of stipules.

Order 57. Sapindales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; stipulate.

Trends: 1. Development of palmately compound and palmately lobed leaves either through shortening of the pinnate rachis or loss of lateral leaflets. 2. Development of simple leaves. 3. Development of Spinose Teeth in *Meliosma*. However, present knowledge of the leaves of the Meliosmaceae is insufficient to allow their systematic placement. 4. Loss of stipules in families such as Aceraceae, Hippocastanaceae, and Meliosmaceae.

Order 58. Geraniales

Leaves pinnately compound; margin entire; venation pinnate; secondary veins camptodromous; tertiary venation percurrent; stipulate.

Trends: To simple leaves with petiolar attachments still persisting.

Order 59. Polygalales

Leaves simple; margin entire; venation pinnate; secondary veins brochidodromous; stipulate.

Trend: Loss of stipules.

Order 60. Cornales (including the Cornaceae, Garryaceae, Davidiaceae, Nyssaceae, Alangiaceae, and Mastixiaceae)

Leaves simple; margin with Rosoid Teeth; venation imperfectly actinodromous or acrodromous; tertiary venation percurrent; glands lacking; exstipulate.

Trends: Loss of teeth in Garryaceae, Alangiaceae, Mastixiaceae, and most Cornaceae and Nyssaceae.

Order 60A. Umbellales

Leaves pinnately compound to lobed; margin with Cunonioid Teeth (*Myodocarpus*); venation pinnate; stipulate with stipules sheathing part of the leaf base.

Trend: To palmately compound leaves having actinodromous venation and margins with Rosoid Teeth.

Order 62. Rhamnales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; glands lacking; stipulate.

Trends: 1. The Leeaceae are pinnately compound with Cunonioid Teeth. 2. To simple, palmately lobed leaves with Rosoid Teeth; actinodromous primary venation and thick, moderately spaced, strongly percurrent tertiary veins (Vitaceae). 3. To simple leaves with Rosoid Teeth, pinnate venation and thin, closely spaced percurrent tertiary veins (Rhamnaceae).

Order 63. Oleales

Leaves basically pinnately compound; margin with Cunonioid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation percurrent; glands lacking; exstipulate.

Trends: 1. To simple leaves with craspedodromous secondary veins. 2. To Rosoid Teeth. 3. Loss of marginal teeth.

Order 66. Proteales

Leaves basically pinnately compound; venation pinnate; secondary veins semicraspedodromous; tertiary venation irregular; exstipulate.

Although basically pinnately compound, proteaceous leaves show no features which definitely relate them to the Rosidae.

Trends: 1. To simple leaves in both subfamilies of Proteaceae. 2. To ternately pinnatifid leaves, some with spinose tips, in the subfamily Proteoideae. 3. To Spinose Teeth and craspedodromous secondary venation in the subfamily Grevilleoideae.

Rosoid Tooth Types

1. *Cunonioid*—C (Figs. 2, 18)—Cunoniaceae, Leeaceae. Tooth with a small, clear glandular apex, with the principal vein to the tooth branching below it, in or near the sinus, and sending one branch to the superadjacent secondary vein or to the sinus and the other branch to the tooth apex on a deflected course along the apical side.

2. *Rosoid*—R (Figs. 2, 18)—Rosaceae, Saxifragaceae. Tooth with a large, clear glandular apical opening (foramen) broadening distally from the sub-apical termination of the usually central principal vein of the tooth. A pair of lateral accessory veins of higher order is connivent with the principal vein, follows a straight rather than a looped course, and terminates in the apical foramen. This tooth is generally broader and more symmetrical than the Cunonioid type.

3. *Spinose*—Sp (Fig. 18)—Meliosmaceae. Tooth with the principal vein projecting beyond its apex.

TABLE 2. Contrast in certain leaf characters between the Dilleniid Asteridae and the Rosid Asteridae. The cross stands for the presence of the named character; dashes for its absence; blanks for lack of data. In the columns where the letter symbols are not explained by the headings: P = pinnately lobed, C = Cunonioid Tooth type, P = pinnate vein configuration, Br = brochidodromous secondary veins, PAd = intercostal venation tending to be oriented parallel to the secondaries and ramifying admedially.

LEAF CHARACTERISTICS									
TAXON	Simple Compound	Pinnately Lobed	Entire MARGIN Toothed	TOOTH TYPE	1° VEIN CONFIGURATION	2° VEIN CONFIGURATION	INTRAMARGINAL VEINS	INTERCOSTAL VENATION	LATEX
DILLENIID ASTERIDAE	S	--	E	--	P	Br	+	P Ad	+
GENTIANALES	S	--	E	--	P	Br	+	P Ad	+
POLEMONIALES	S	--	E	--	P	Br	+	P Ad	+
RUBIALES	S	--	E	--	P	Br	+	P Ad	+
CAMPANULALES	S	--			P				+
ASTERALES	S	--	E	--	P	Br	+		+
ROSID ASTERIDAE	C	P	T	C	P				--
LAMIALES	S		T	C	P				--
SCROPHULARIALES	C	P	T	C	P				--
DIPSACALES	C	P	T	C	P				--

SUBCLASS G. ASTERIDAE

Although our survey of the leaves of the asterid families is as yet preliminary, our data indicate that the leaves of this subclass can be divided into two fundamental categories; one group most closely resembling the Ochnales-Myrtales (Fig. 12), which we call the Dilleniid-Leafed Asterids and the other most similar to those of Saxifragales-Araliales, which we term the Rosid-Leafed Asterids (Fig. 17). The basic leaf features of these two groups are summarized in Table 2 and in more detail below. The ordinal breakdown is that of Takhtajan with minor modifications after Cronquist. The status of stipules has not been analyzed in sufficient detail to determine whether they are basic to the orders or are of secondary origin within them; thus they have been omitted from consideration in this treatment.

I. DILLENIID-LEAFED ASTERIDS

Leaves basically simple; margin entire; venation pinnate; secondary veins strongly brochidodromous and tending to form an intramarginal vein (Fig. 19); intercostal venation tending to be oriented parallel to the secondaries, in ochnalean fashion; latex present (Table 2). In addition, this group tends to have interxylary phloem and vested pits.

Order 68. Gentianales (excluding Rubiaceae after Cronquist, 1968)

Leaves simple; margin entire; venation pinnate; secondary veins brochido-



FIGURE 19. Ochnalean venation in the Gentianales; *Chilocarpus decipiens* Hook. (Apocynaceae); Sumatra: *Toroes* 1428 (UC); $\times 5$.

dromous, tending to form an intramarginal vein; tertiary venation tending to parallel the secondaries; latex present (Fig. 19).

Order 69. Polemoniales (including Solanaceae and Nolanaceae, after Cronquist, 1968)

Leaves simple; margin entire; venation pinnate; secondary veins strongly brochidodromous, tending to form an intramarginal vein; tertiary venation often paralleling the secondaries; latex very rare, known only in a few genera of the Convolvulaceae.

Order 69A. Rubiales (after Cronquist, 1968)

Leaves simple; margin basically entire; venation pinnate; secondary veins brochidodromous, tending to form intramarginal veins; tertiary venation oriented parallel to the secondaries; latex absent; stipulate.

Order 72. Campanulales

Leaves simple; margin entire; venation pinnate; secondary veins and higher order venation not determined for this study; latex present.

Order 74. Asterales

Leaves basically simple, when compound either pinnatifid or of pinnatifid origin by deeper dissection of an originally simple blade; margin entire; venation

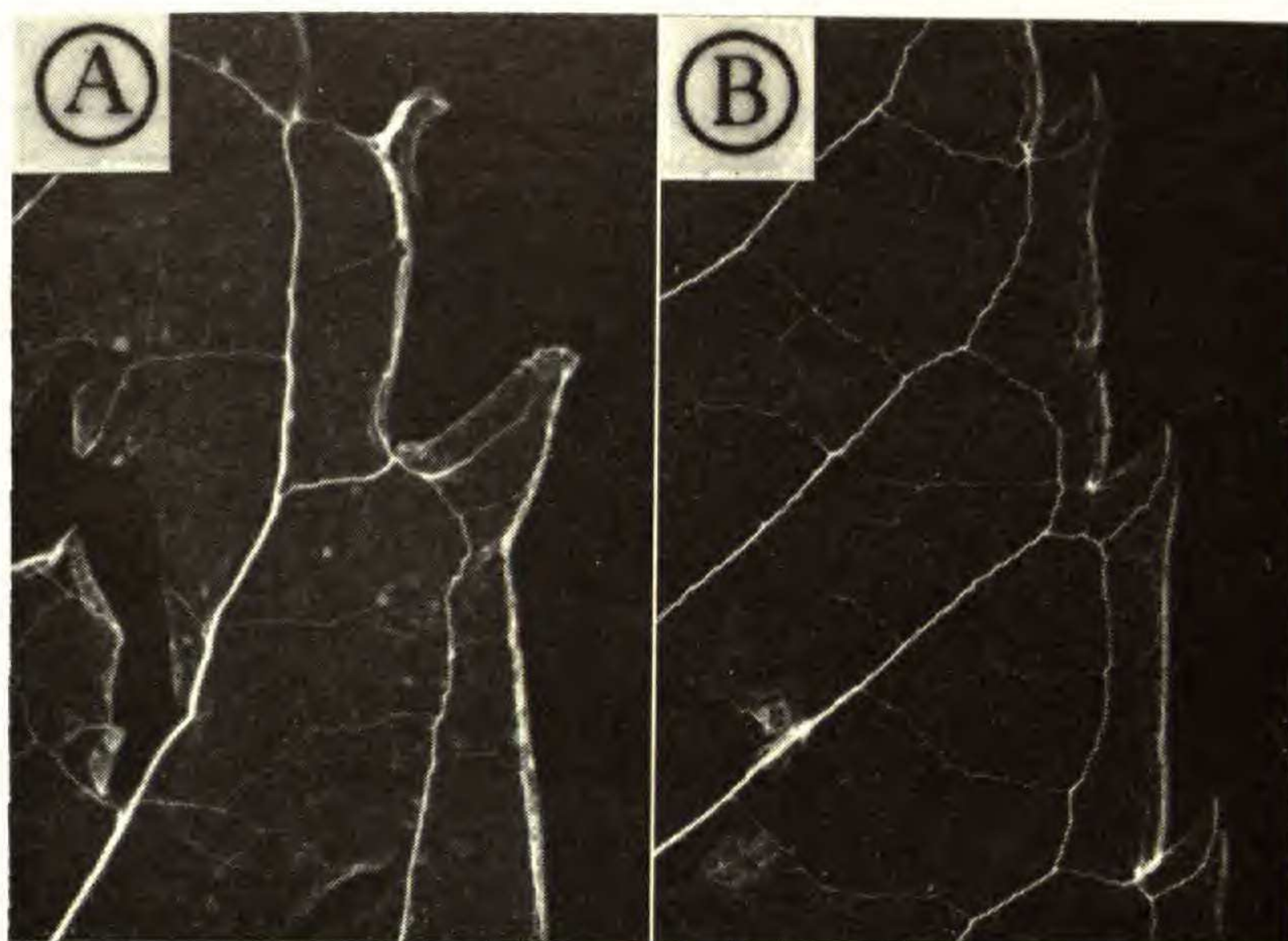


FIGURE 20. Inferred Cunonioid Teeth in the Scrophulariales; $\times 5$.—A. *Tecoma stans* Juss. (Bignoniaceae); Nicaragua: Smith s.n. (UC 975382).—B. *Campsis chinensis* (Lam.) Voss. (Bignoniaceae); China: Kangsi, Ip s.n. (UC 258798).

pinnate; secondary veins brochidodromous and tending to form an intramarginal vein; tertiary venation various; latex present.

II. ROSID-LEAFED ASTERIDS

Leaves basically pinnately compound; margin with Cunonioid Teeth (Fig. 20); venation pinnate; secondary veins often semicraspedodromous; tertiary venation transversely ramified; latex absent. In addition interxylary phloem is absent except rarely in the Acanthaceae and very rarely in the Myoporaceae. Included phloem of the concentric type does occur in the Verbenaceae.

Order 67. Dipsacales

Leaves mostly simple except pinnately compound in *Sambucus* of the Caprifoliaceae; margin with Cunonioid and Rosoid Teeth; venation pinnate; secondary veins semicraspedodromous; tertiary venation transverse; latex absent.

Order 70. Scrophulariales (excluding Solanaceae and Nolanaceae after Cronquist, 1968)

Leaves pinnately compound; margin with Cunonioid Teeth (Fig. 20); venation pinnate; latex absent.

Order 71. Lamiales

Leaves basically simple, margin with Cunonioid Teeth; latex absent.

CONCLUSIONS

The data which we have presented here demonstrate that a number of lower order leaf architectural features, including leaf organization, configuration of the first three vein orders, and characteristics of the leaf margin are significant sys-

tematic indicators within the dicotyledons. We have shown that when variations in these characters are analyzed using the classifications of Takhtajan and Cronquist, they yield, with certain exceptions, a generally coherent arrangement, which we feel reflects the basic soundness of these classifications as approaches to a natural system.

Looking at their most obvious feature, dicot leaves display a rather general separation into four basic patterns of organization: simple, pinnately compound, palmately lobed, and palmately compound. However, when analyzed in terms of the Takhtajan and Cronquist systems and in conjunction with variation in their vein configuration and marginal features, each of these forms can be seen to have arisen several times. Each line, however, often retained characteristics which betray these separate origins (Fig. 21). Thus simple leaves are found in the Magnoliidae, Caryophyllidae, Pinnate Dilleniidae, the so-called "Dilleniid-Leafed Asterids," as well as in the other subclasses, as reductions of the compound condition. However, the affinities of the simple leaves in each of these subclasses can be recognized by a combination of higher order architectural features such as vein disorganization or the presence of intersecondaries in the Magnoliidae, obsolescence of venation above the fourth order and a trend to imperfect actinodromy or acrodromy in the Caryophyllidae, or by a characteristic tooth type and course of the secondary and tertiary venation in the other subclasses. Pinnately compound leaves seem to have developed separately in both the Ranunculidae and the Rosidae, the distinction between them being in their respective tooth types and primary and secondary venation. Palmately lobed leaves are seen in the Hamamelididae, the Palmate Dilleniidae, and in the Rosidae, the basic differences in venation and characters of the marginal teeth showing the fundamental separation of these taxa. Palmately compound leaves are known principally in the Palmate Dilleniidae, less often in the Rosidae and only very rarely in the Hamamelididae.

Apparent also from the preceding survey is the stability of many of the tooth types found in dicot leaves. Recognition of these tooth types thus appears to be an overlooked tool of major systematic importance. Of the various types, the Chloranthoid Tooth in the Ranunculidae, certain Magnoliidae, and some of the Hamamelididae; the Theoid Tooth in the Dilleniidae; and the Cunonioid Type in the Rosidae are the most important. Classification of tooth type is of great significance in the systematic recognition of leaves at higher taxonomic levels, and the determination of a number of characteristic variations in tooth type

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FIGURE 21. Summary of dicot leaf relationships. Basic leaf types of the various subclasses are indicated by the drawings. Note that only the Rosidae and the Rosid Asterids have basically pinnately compound leaves and that the Asteridae have two apparently separate leaf affinities. The Dilleniales are shown as an early and isolated offshoot of the Dilleniid stock distantly related to its later elaboration. The basal leaf in the Hamamelididae represents the Cretaceous fossil group termed the "Platanoids" and the pinnatifid leaf in the Rosidae represents the middle Cretaceous genus *Sapindopsis*, which possibly has affinities to the basal Rosidae. Basic tooth types shown are: Ch = Chloranthoid, P = Platanoid, C = Cunonioid, D = Dillenioid, T = Theoid.

appears to be an important key in ascertaining patterns of evolution in the various groups.

The persistence and stability of these tooth types through extensive taxonomic reaches of the dicotyledons has further and rather unexpected implications for the determination of angiosperm evolution. Work by Sinnott & Bailey (1915), Bailey & Sinnott (1916), Chaney & Sanborn (1933) and Wolfe (1971) showed that the great majority (75–90%) of tropical rainforest leaves have entire margins. This percentage decreases to near equality in the upland tropics and subtropical forests, while the leaves of temperate forests are mainly non-entire. Leaves of arctic, alpine, and xeric environments are predominately entire-margined.

Our observation of the persistence and coherence of tooth evolution patterns from a portion of the Magnoliidae and into the Ranunculidae, Hamamelididae, Dilleniidae, Rosidae, and possibly what we have called the “Rosid-Leafed Asteridae” (Fig. 21), may indicate that most of the important innovations in dicot radiation leading to major shifts in adaptive strategy could not have taken place in a setting analogous to that of the present tropical rainforest. It seems possible that in the rainforest setting the survival of microscopic adaptations and the process of extreme niche partitioning have given rise to a great diversity of species, but the region may, in general, be a “phyletic sink” compared to more extreme humid climatic regions. In more extreme environments a premium on macroscopic adaptation may result in more radical shifts in adaptive strategies leading more rapidly to novelty at higher taxonomic levels. An exception to this picture is, of course, the Ochnalean Dilleniid Alliance where teeth seem to be lost near the base of the line.

This analysis also resolves the assignment of certain taxa about which there is doubt or disagreement between the treatments of Takhtajan and Cronquist. For example, due to its basically pinnately compound leaf form the Ranunculidae are retained as a separate subclass as by Takhtajan (1969), but the Illiciales, with simple leaves, are moved to the Magnoliidae as by Cronquist (1968).

Leaf data also appear to support Takhtajan’s assignment of the Euphorbiales to the Dilleniidae. Leaves reinforce Cronquist’s assignment of the Lecythidaceae and related families to the Dilleniidae, rather than to the Rosidae as in Takhtajan; the erection of two orders for Takhtajan’s (1969) order Cornales; and the assignment of the Solanaceae to the Polemoniales rather than to the Scrophulariales, as by Takhtajan. In addition, our analysis suggests the reassignment of several “problem” families like Didymelaceae to the Dilleniidae, as well as reinforcing the assignment of the Medusagynaceae to that subclass by both authors.

On the other hand, certain areas where the leaf data are anomalous in the light of the Takhtajan and Cronquist systems should lead to a careful reevaluation of all morphologically and systematically significant features and of the assumptions of the systems themselves in order to resolve the conflicts. The most important of these are our reassignment of the Juglandales to the Rosidae, the strong leaf architectural affinities of the Celastrales and Myrtales to the Pinnate-Leafed Dilleniidae, and the apparent fundamental separation of the leaf architectural patterns of the Asteridae into two groups, one having Ochnalean-Myrtalean leaf affinities and the other having an apparent Rosid pattern. Numerous other

leaf groupings which we have made at lower taxonomic levels must be similarly evaluated.

For the purpose of a comparison of leaf architectural features with degree of phylogenetic advancement, we take as our assumption, as Takhtajan and Cronquist did, that the Magnoliidae as a whole represent a residuum of the most primitive features among the living dicots. Starting from this, the simple, entire, pinnately-veined leaf with somewhat irregular camptodromous secondary venation, and irregular tertiary and high order veins appears to be most primitive among living leaves; and the non-entire, lobate, and compound leaf appears to be more advanced. This observation accords with Lower Cretaceous fossil evidence of dicot evolution reviewed by Doyle & Hickey (in press).

Finally, this paper provides the first framework for a systematic summary of dicot leaf architectural features and for the development of a regular systematic method for their identification. Not only will this be of importance for the determination of modern leaves but will also make possible the identification of dicot leaf fossils at higher taxonomic levels, thus leading to significant contributions in deciphering the phylogeny of angiosperms from their fossil remains.

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